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ENVIRONMENT AND HEREDITY

No. 36

ENVIRONMENT AND HEREDITY

by

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PREFACE

THE plan of this book is such that the earlier part is designed to provide the scientific background essential to an understanding of the later chapters. The reader may, however, prefer to take the last chapter, perhaps even the last three chapters, first, in order to see whither the argument leads, and then turn back to the earlier part.

I have to thank Mr. J. F. Duff of the University of Durham, Professor G. H. Thomson of the University of Edinburgh, and the Editor of the *British Journal of Psychology*, for permission to quote the tables and figures in Chapter VIII. from the article on "The Social and Geographical Distribution of Intelligence in Northumberland."

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INTRODUCTION

When reference to heredity is made in conversation or in fiction it is frequently of a sinister nature, and suggests that heredity is an inescapable fate and a burden which one generation lets fall upon the shoulders of the next. Similarity of misfortune in successive generations is described as a hereditary curse, and we find laments that, in spite of all efforts, " bad will out." We hear of families like the " Jukes," a record of whose misdeeds and crimes, over several generations, could fill a large volume. As the brighter side of the picture, we hear of striking resemblances between men and women and the portraits of handsome ancestors, and of families famed for beauty and brains.

People are generally surprised if children do not resemble either parent. If, on the other hand, the children resemble them very strongly, this also is a subject of comment. Children's shortcomings are despairingly commented on by parents in such terms as, " I don't know whom he takes after, he certainly doesn't get it from my side " ; but there may be little knowledge of the ancestry whose integrity is assumed. How little knowledge we possess of even grandparents and great-grandparents will surprise most of us who pause to think of the matter.

We hear disappointed people talk of what they could have done if they had " had their chance." Such regrets often lead to vague discussion whether heredity or environment is of greater importance. There is a fairy story which has a moral for those who venture to pronounce upon the relative influence of heredity and environment. It tells of a prince in captivity who by means of a magic crystal saw where his lost princess dwelt and that she loved him. Hidden by a cloak of invisibility he escaped his captors, and on a magic carpet which floated through the air he arrived beside the princess in time to save her life. The donors of the three gifts—crystal, cloak, and carpet—fell to arguing which was the most important. Evidently they were equally important ; one would have been useless without the others. Similarly environment and heredity are complementary. Without inheritance there would be no organism at all, and without environment it could not exist for a fraction of a second. Under certain conditions, however, which will be discussed, it is possible to estimate, in some cases, the relative influences of heredity and environment.

Many philanthropists have contended that the inequalities between men are due to circumstances, and could be abolished by education. We shall question and examine the validity of this view, which is obviously at variance with the opinion of those who regret the falling birth-rate of the so-called "upper classes" compared with the fertility of the so-called "lower classes," believing that the latter's hereditary weakness can never be improved to the level of the former's hereditary strength.

Many men's political views and ideas on the organization of society imply unrecognized and unacknowledged beliefs about inheritance. Some believe in a stable communal hierarchy, each grade of which requires a different kind of education. They consider the wealthy classes to be the most intelligent and deserving of the most expensive education. Others believe that great ability may spring from any stock, and is no more likely to be found in one type than in another. Some hold that everyone's ability can be increased and the level of national intelligence raised by education, and that the self-improvement of one generation is handed on to the next. They would answer in the affirmative the old proverbial question, "Can a father bequeath his learning to his son?" In other words, they believe in the inheritance of acquired characters.

We hear that the good old days have gone and that children are not what their parents were. Side by side with this contention there is, curiously enough, a widespread belief in human progress. In what does this supposed progress consist? Are we biologically superior to our forefathers? Or has there been retrogression?

Children are sometimes considered the victims of their parents' circumstances, as if they inherited bodily deficiencies resulting from accident to the parent or from the nature of his work. Not long ago I heard some children's ill-health explained (quite falsely) by the fact that the father suffered from gas poisoning during the war. This is complete acceptance of the doctrine of inheritance of acquired characters—a subject which will be considered in Chapter IX.

When children of parents in unhealthy trades are found to be unhealthy, this is frequently cited as an example of inheritance of the environmental effect. The probable explanation that healthy men get the better jobs and that the parents have been driven to a poor occupation *because of their poor physique*, which the children inherit, is given scant consideration. Cause and effect are difficult to disentangle and associate correctly. The case of the baby and the comforter has a good moral. A health worker laid stress on the fact that babies having comforters (" dummies ") were on the average less healthy than those without them, and expected his audience to accept this as a definite instance of cause and effect. Comforters *are* most probably bad for babies, but there is further evidence to be considered. Perhaps the babies were already unhealthy and therefore fractious, and were consequently given comforters to keep them quiet. What of the mothers of these unhealthy babies ? Perhaps they too were unhealthy, and the children inherited some of their weakness. A weakly mother would more easily yield to the temptation of the comforter because she could less endure the irritation of a crying baby. Cause and effect are indeed difficult to determine.

There are innumerable questions on this subject of heredity ; there are more questions than answers. The bearing of the facts on society is often most obscure. In a short treatise such as this it is impossible to deal exhaustively with the subject. The kind of work that has been and is being done can be indicated. Facts can be stated and a discussion of their social implications can be at least initiated.

ENVIRONMENT AND HEREDITY

CHAPTER I

EVOLUTION

THE question of human progress is most interesting and many-sided. Many no doubt feel that, though pessimists may talk about the decadence and decline of our civilization, there has, on the whole, been progress. Comparing ourselves with the ancient Britons, who dyed themselves with woad, wore skins, and worshipped strange gods, they feel convinced of progress. If it were pointed out that this progress may be one of external achievement only, involving no innate improvement, the optimist might reply by asking, " Isn't man a product of organic evolution and doesn't that imply continual progress?" Man is indeed a product of organic evolution, but the second half of the question cannot always be answered in the affirmative. Perhaps it is here desirable to enlarge somewhat on "evolution." According to a theory of organic evolution such plants and animals, including man, as exist to-day, are not only the descendants of previously existing ones, but have, in the course of descent, undergone modification, *i.e.* alteration in structure. Some ancestors were very different from their present descendants; from a single ancestral type many different lines of descent have been traced. This theory of organic evolution is founded on evidence of various kinds. The primary and direct evidence is that furnished by the study of fossil forms (palæontology). When plants and animals die, their bodies or parts of them are, under certain conditions, preserved as fossils. Favourable conditions exist under water, on lake and ocean floors, where silt continually falls to form mud or ooze which becomes compressed into rock. In successive strata the nearer the rocks are to the surface of the earth's crust, *i.e.* the more recent they are, the more do the fossil forms found resemble plants and animals alive today. Some species of fossil plants of tertiary deposits —dating from a time before there were any men on the earth—are identical with present-day species. For many plants and animals we can find not only the comparatively recent but the very remote ancestors, or at least the ancestral types, from one of which the present-day representatives have in all probability evolved. Perhaps the most perfect record of ancestry is that of the horse, which can be traced back by fossil remains in different strata of the earth's surface to a type of little five-toed animal, called *Phenacodus*, about three feet high. This fossil animal was not recognized as the ancestor of the modern horse until several intermediate stages had been discovered. The ancestry can now be traced showing the progressive change from five toes to one, whose enlarged nail the horse's hoof represents. There has been lengthening of the limbs, change in the type of joints, consolidation of the bones in the lower parts of the legs, and alteration in the type of teeth. The changes resulted [illegible] a creature more fitted to the environment in which [illegible] lived.

The existence in the rocks of fossils proving the previous existence of animals and plants very different from existing ones was serious evidence against the fundamentalist view, *i.e.* the literal interpretation of the story of creation in the first chapter of Genesis. Extravagant theories of " catastrophism " were brought forward to explain the presence of the fossils. It was suggested that the world had experienced vast local cataclysms which had destroyed all living things over large areas ; these parts of the earth had then been repeopled by plants and animals spreading from neighbouring parts. Later, separate creations were postulated to account for the different types of plants and animals found in the successive layers of the earth's crust, the previous types being supposed to have been destroyed by cataclysms. It seems obvious to us now that such theories have no ring of truth. What are we to think of the suggestion of another writer, unwilling to question the literal truth of Genesis, that Providence placed the fossils in the rocks to rebuke man's curiosity ? The only satisfactory explanations of the existence of fossils is a theory of organic evolution.

Interesting fossil evidence for evolution is that of so-called " missing links," such as the fossil animal *Archæopteryx* of the Secondary period, which has points of resemblance to both reptiles and birds.

The forms of existing plants and animals, and their distribution, also present us with facts which only a theory of organic evolution can satisfactorily explain. It was, indeed, facts of distribution which first suggested the idea of evolution to Charles Darwin during the voyage of H.M.S. *Beagle* (1831–36). He was impressed by the similarity, but not the identity, of form between the turtles of the mainland of South America and those of the Galapagos Islands about six hundred miles to the west. Similarly with other animals, each island had its own characteristic form slightly differing from forms on the other islands and on the mainland. He recognized them as " blood relations " descended from a common ancestor and modified differently in the course of their descent in the isolation of the different islands. He felt himself brought near to the " very act of creation "—not a " once and for all " creation but the " creation " of new species by descent, with modification, from previous ones. It is now generally recognized how important a factor isolation can be in both biological and cultural evolution.

When the anatomy of animals is compared we find overwhelming evidence for evolution. The fore-limbs of all backboned animals are made according to a similar pattern. They have the same general plan as regards bones, nerves, muscles, and blood vessels, although their outward form and function may be very different. Darwin commented on these facts thus, " How inexplicable would be the similar pattern of the arm of a frog, the paddle of a turtle, the flipper of a whale, the wing of a bat, the arm of a man, as independent acts of creation, and how simply explained as the varying descendants of a single progenitor." Similarly, the fact that the long neck of the giraffe and the almost non-existent one of the whale have the same number of vertebræ would seem inexplicable if they were due to independent acts of creation.

Evolution, moreover, offers the only reasonable explanation of vestigial structures which never reach full development, and either remain useless or perform a function differing from their original ancestral one.

They represent structures which were fully developed in remote ancestors. Examples are the vermiform appendix on the large intestine of man, and the small bones in the whale representing undeveloped hind legs.

Embryonic development, too, is suggestive of evolution. During the development of the embryo from the fertilized egg, stages can be recognized which are similar to adult forms in simpler or more primitive organisms. More recent evidence of evolution is that afforded by blood tests.

A doctrine postulating special creation of each different kind of animal and plant has no scientific evidence whatsoever to support it. On the other hand, there are many details concerning, for example, fossil forms, distribution, comparative anatomy, and embryology which fall into rational order when explained in terms of organic evolution, and which would otherwise be a chaos of unrelated facts. No other explanation will fit these facts, and they thus constitute evidence that evolution has taken place. On the whole, evolution has moved from relatively simple types to more complex ones—but this is not a universal law. Many lines show degeneracy—there are many simple organisms which are recognized as descendants of more complex ancestors. Many degenerate descendants show their degeneracy (*i.e.* a lesser degree of organization) both in structure and in mode of life ; as, for example, the fungi, which are not only less highly organized in structure but also, like lazy intruders, leave to their hosts the task of providing for their needs. Moreover, in the evolution of a single species one part may degenerate and others become more complex. It is natural to inquire into the means by which this gradual evolution has been brought about. To suggest that evolution is to be explained merely as the working out of a creator's preconceived plan is, scientifically speaking, to offer no explanation at all. It seems, moreover, unreasonable to postulate a directive agency like our own minds, even though on a grander scale, behind evolution. The innumerable "mistakes" and the creation of degenerate types would be little credit to such a mind. Why should some birds have been created with degenerate wings and no power of flight? Excessive size having proved a failure, it would seem unintelligent to create fresh types with the same disadvantage doomed to failure after a short trial.[1]

Of the scientific theories some have attributed evolution simply and solely to the operation of the laws of heredity, to the inevitable development of the organism's tendency to vary in a certain direction. This extreme view is now rarely, if ever, held; and important rôles of various kinds are attributed to the environment by exponents, on the one hand, of Lamarckism (the theory of J. B. Lamarck, 1744–1829), and, on the other, of Darwinism. According to the Lamarckian view, changes induced in plants and animals by external forces are handed on at least in part to the descendants. It is common knowledge that factors such as moisture and light or shade affect the growth of plants. With animals, not only the environment but also the animals' efforts (or lack of effort) have their effect on development. A blacksmith's muscles develop with use; the sedentary worker's muscles get flabby unless he makes an effort to take exercise. In other words, the body becomes modified by use or disuse.

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[1] Unfortunately we cannot enter here into serious discussion on the philosophical aspect of the question.

There have been vast changes in the climate and in the physical features of the earth. Changed environment brings new needs which call forth fresh efforts. Lamarck contended that the effects of use and disuse were inherited, and thus was evolution brought about. At present no further consideration will be given to this view, which the majority of biologists do not support. Darwin's views, with some modification, are much more generally accepted. Nevertheless tacit acceptance of the Lamarckian idea (the inheritance of acquired characters) is fairly common in the popular mind, and further discussion of the question will be deferred until Chapter IX.

There are three sovereign principles in the Darwinian theory of evolution: variation, heredity, and natural selection. It is observable that not all members of a family, or species, are alike, *i.e.* variation exists. It is not necessary at this stage to inquire into the origin of such variation, but merely to accept its existence as a fact. With regard to heredity, it is also an observable fact that in some cases a variation is handed on to subsequent generations.[1] With regard to the third principle—natural selection—observation of plants and animals under cultivation and domestication is illuminating. The breeder of plants and animals keeps his eyes open for little differences between individuals, some of which prove heritable. By choosing, for breeding purposes, individuals showing variation in a direction which he desires, he can produce different varieties. In the course of his work he may discard far more than he keeps. It must be clearly understood that he cannot induce such variations as he desires; he can but choose from the variations which happen to occur. The cause of origin of the variations is not known ; their nature will be discussed in subsequent chapters. There is no evidence that they are adaptations to environment. Indeed, modifications due to the environment, such as increased growth due to manuring, are not heritable. The breeder may be said to practise artificial selection. Darwin asked himself whether or not there was in wild nature any process comparable to such artificial selection, and his observations led him to a realization that there was. He observed the prolific nature of many species, and their consequently enormous death-rate, which must undoubtedly involve selection. The fertility of many species is amazing, that of oysters and of herrings being proverbial. Even elephants, which are very slow breeding animals, could in time produce enormous numbers if all survived. Darwin estimated that, assuming an elephant to breed for the first time at the age of thirty years, and to live to a hundred, producing six young during this time, then, if all the animals survived and lived to reproduce similarly, after about five hundred years there would be nineteen million elephants descended from the single pair. Among quicker breeding animals and plants much more sensational figures can be obtained. A poppy, for example, produces thousands of tiny seeds, as does an orchid, whose seeds are so fine that they are carried like dust in the wind. If all the seeds grew into plants there would very soon be no room for anything else. When experimenting with a Rotifer, a minute barely visible organism that breeds very rapidly, Punnet calculated that if all the eggs of the sixty-seven generations produced in about a year had survived and grown into adult animals, then their total volume would have been greater than that of the earth. In most species, indeed, there is a gigantic death-rate—the majority of organisms die young. There are factors in nature that keep the numbers down. Space and food supply are limited ; there is a struggle with unfavourable environment, with other animals, both of the same and of other species. There is thus a general struggle for existence, and not all those born are able to survive. But, the recurrence of variations being an established fact, it seems reasonable to suppose—and can be demonstrated—that the death-rate is, on the whole, not random but selective. If an organism varies in any manner, however small, that is favourable to itself, it will tend to survive, *i.e.* be naturally selected, and less fortunate ones will tend, in time, to become less numerous or even to disappear. In this way a new species can be established, and those not conforming to a certain standard of efficiency will be cut off, leaving little or no progeny. Natural selection thus results in a type more fitted to its environment, but it does not necessarily lead to greater complexity of organization. Darwin explained the presence on certain oceanic islands of short-winged beetles more or less incapable of flight, by the fact that they are safe from the effect of high winds, which carry out to sea and to destruction those with long and well-developed wings. Generations of long-winged ones would thus be eliminated, while short-winged ones would survive, and in so far as the variation was hereditary, would perpetuate this quality.

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[1] See Chapter II.

In answer to the " optimist's " question at the beginning of this chapter,[1] we now see that evolution does *not* necessarily imply progress of organization and development. What it does imply is greater fitness for the environment. But what of the environment ? We must not suppose that it has any divine right as compared with the organism which has been compelled to adapt itself to it, perhaps at the expense of a nobler line of development. Particularly is this true of man. If in his case, too, survival is the criterion of fitness, we are bound to consider of what kind is the environment, adaptation to which is to be rewarded by greater hopes of survival. While, as Arthur Thomson aptly expressed it, "the tapeworm is as well adapted to its inglorious lot as is the lark at heaven's gate," there is a world of difference between the dignities of their estates. Heaven's gate is, figuratively speaking, the environment in which man should be fitted to survive.

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[1] See page 13.

In outline the theory of evolution by natural selection seems so simple that we wonder why it was not thought of earlier. It is significant that it did occur independently to two contemporaries, Charles Darwin and Alfred Russell Wallace, both of whom, already deeply conscious of the incessant and universal struggle for existence, were greatly impressed by their reading of Malthus, *On Population.* But the task of tracing the course of natural selection is far from simple. It can be analysed into various aspects, an important one, for example, being parental care. An animal which abandons its young at the approach of danger may itself survive, but will leave fewer progeny to the next generation, and thus will tend to be eliminated as a type.

Natural selection would appear to be the simplest and most generally accepted interpretation of the method of evolution. The environment has a moulding influence —it sifts, selects, and rejects. Its role is passive, in that natural selection consists in the elimination of the unfit, leaving place for the fit. The theory of natural selection offers no explanation of the cause of the heritable variations. It accepts their existence as a fact, and shows how the environment can bring about evolution by working on them. To speak of them as spontaneous is but to express ignorance of their origin. There may be something within the organism which determines variation in a given direction, but it must not be forgotten that observation of variation under domestication shows a large number of variations in different directions. There is a limit to the kind of variations one can expect ; we should be legitimately surprised to find men developing feathers or fish growing fur. Variation will be more readily understood after consideration of Mendelism.

There is no evidence that the variations are attempts at adaptation to the environment ; such adaptation results from the elimination of those which are less well fitted to the environment. Considering our ignorance, categorical statements attributing specific purposes to parts of plants and animals are frequently unfounded or, at least, misleading. Such statements are often anthropomorphic in conception, and speak of that which God or Nature intended or did not intend. It is more correct scientifically to speak of function, not of purpose. If a part fulfils a useful function it will most probably have survival value, *i.e.* it will promote the survival of the possessor. Even the term " adaptation " is itself misleading, for it seems to carry with it the suggestion of conscious endeavour or conscious shaping towards an end ; whereas out of a number of variations which may occur in different directions the environment allows to survive only those which " fit," others dying because they are not so fit for their environment and there is not room for all. As the process of selection is going on all the time, it will act on successive generations and presumably in the same direction, and thus an adaptive character can be built up. Animals in cold regions have thick fur—this is an adaptation to surroundings, not because they have felt the cold and decided to grow more fur, but because those with less thick fur have tended to die out, leaving only those with suitable covering to perpetuate that type. Pigment in the skin is a protection against sunlight, and up to a certain point is developed under the influence of sunlight. Dark-skinned human races are found where sunlight is strong, but there is no evidence that this is a progressive darkening by the inheritance of the acquired character. Rather are we to attribute their distribution to the fact that they, by virtue of their colour, have survival value for that environment, while lighter-skinned races can survive in other environment, and may possess other factors of survival which establish their ascendancy in the areas where they are found. It is often difficult to see what character or characters have led to survival, but sometimes it is clear enough. There are numerous examples in insects of colouring which, by making the possessors fit into the background, renders them less liable to detection, and has an obvious survival value. Observers have been able to count the greater number of victims among those not adequately fitting in with their surroundings.

Having considered the evidence for evolution, and its probable methods of working, it is now time to return to the question of man and his evolution and progress.

There is ample evidence that man, too, is a product of evolution. The evidence comes from fossil records, comparative anatomy, embryology, and blood tests. However, lest the answer to the original question concerning the innate superiority of ourselves compared with the ancient Britons should be assumed to be answered in our favour, one important factor in evolution must be strongly emphasized. This factor is time. Length of time during which there have been men on earth is short compared with the time which has elapsed since life first appeared. Moreover, the whole period of history is short compared with the period during which men have inhabited the earth. A few *approximate* figures may illustrate these facts. The history of the earth is more easily described in terms of geological sequence rather than of chronological time. Geologists are usually loth to commit themselves to dates. Sequences of biological development can, by means of fossil remains, be traced either backwards or forwards, but in all cases it is much easier to assign stages of development to different geological strata than to definite, or even approximate, points of time. The uncertain nature of all these figures must be realized; they serve to give an approximate basis of comparison.

There have been various calculations—based largely on the facts of radio-activity—as to the probable age of the earth. The oldest known rock of the earth's crust is probably as much as 1,500 million years old, and life is considered to have begun on earth about 1,000 million years ago. But the fossil record is probably only half as old, presumably because the earlier animals did not form skeletons which would lend themselves to fossilization. The earliest known fossils are fairly complex organisms; we cannot get a fossil from an amœba, or even from a jelly-fish.

The origin of man was late in geological history. *Perhaps* a million years ago the most primitive known types of men now extinct, such as the Peking man

(*Sinanthropus Pekinensis*) and the Java man (*Pithecanthropus erectus*), inhabited their respective lands. Such men were ape-like compared with modern men, who are classified as *Homo sapiens*. The name *Pithecanthropus* indicates an intermediate position between apes and men (Greek, *pithecos* = ape; *anthropos* = man), and the specific name "*erectus*" was given because the shape of the thigh bone indicates an erect posture. Such types are, according to some classifications, called Prehominids. Prehistoric men are known by their skeletal remains and by their implements and other evidences of culture they have left behind. Huxley and Haddon suggest that a type of culture known as the Chellean *may* have begun about half a million years ago, and the Mousterian culture about fifty or one hundred thousand years ago. Even this latter culture is not associated with *Homo sapiens* but with a type known as Neanderthal man (*Homo neanderthalensis*). The same authors suggest that in Europe the Aurignacian culture, associated with varieties of *Homo sapiens*, may not be more than twenty to forty thousand years old. However, very recent investigations associated with the finding of a prehistoric human skull at Swanscombe in Kent suggest that *Homo sapiens* may have had a very much earlier origin, and some kinds of men so far developed as to merit this name may have existed at the same time as, or earlier than, the men of the above-mentioned Chellean culture. Anthropology is a complicated subject, and it suffices here to say that, even though man's appearance on earth is, geologically speaking, late, it is a long time ago in terms of historical time, whether we accept the earlier or the later time suggested for the appearance of *Homo sapiens*.

Now the earliest historical records are round about

3000 B.C. or a little earlier. The whole historical period of little more than 5,000 years is, compared with the age of the earth, like a day in a thousand years. It represents a fraction of man's time on earth ; though, by what has been said of the doubt concerning human origins, we do not know what fraction, it is certainly not a large one. Great changes in type are not to be expected within a period comparatively so short. During the evolution and early development of the human type there must have been great changes due to natural selection. There is little, if any, evidence of upward change in inherited constitution during the whole period of history.

If there has been little change in man's type for thousands of years it is partly because there has been, for thousands of years, little pressure of natural selection to force up the level. The countless violences that history records have little, if any, selective value. In a primitive society the physical and mental qualities are kept up to a high level by the pitiless elimination of the unfit. In a primitive hunting community even short sight may mean violent death or starvation. Some change in type may have taken and may be taking place owing to the selection of various characters for survival ; such change is, however, small and insignificant in comparison with the vast changes in human achievement, and in the environment which man has created for himself. The characters on which selection might act should be more readily understood after consideration of the facts of inheritance in the following chapters, selection itself being considered in Chapter VI.

Probably few characters which biologically alter a nation are either fostered or eliminated by natural selection in a " civilized " community. Some authors have taken an extremely serious view of the deleterious effect of removing the pressure of natural selection. They regret that superiority no longer profits from the rewards of superiority, since it is as profitable to be unfit as fit, and pessimistically they anticipate the biological decline of "civilized" peoples owing to adverse selection. This point of view will be considered later.

Returning for a moment to the question at the beginning of this chapter about the differences between ourselves and the ancient Britons, they are admittedly to some extent biological, but as such are probably due largely to invasions of foreign "blood" and to intermarriage. The primary difference, however, is that of the *external* heritage of achievements. We have now more knowledge and power over nature, and this knowledge has accumulated through many generations.

If, again, we compare ourselves with the Anglo-Saxon inhabitants of these islands, the differences in behaviour due to different accepted traditions are evident. J. B. S. Haldane draws the interesting comparison between the Vikings and the present-day Scandinavians. There has been very little immigration into Scandinavia, so that here we have a race practically uncontaminated for the last two thousand years (not, it may be said, a pure race—no such thing can be said to exist and probably did not exist even in prehistoric days). A thousand years ago the Scandinavians were skilled warriors ; now they are largely pacifists and mild socialists. This does not, of course, mean that they lack courage, though some contend that, as the most enterprising have left the country, the race has degenerated by adverse selection. No, the most reasonable explanation would seem to be that the traditions have altered, the ideals have changed.

It is often extremely difficult to distinguish between the inheritance of a tradition and true biological inheritance, between change in tradition and biological change. It is hoped that further chapters may help in the sorting out of these problems. It is naturally of the utmost importance to discover the processes of selection which may be at work in a civilized community, and which may slowly be altering its innate constitution, and to inquire if any such processes are likely to lead to betterment. In order to try and answer these questions we must inquire into the nature of inheritance ; and this will be our consideration in the next chapter.

CHAPTER II

HEREDITY : MENDELISM

A NUMBER of isolated facts concerning inheritance must be known to many people. On the other hand, a number of supposed facts and fallacious explanations are also current. Most people can probably recall to mind some instance of a character said to run in a family. The reappearance of the character and the preservation of its identity arouse interested comment, presumably because they are considered unusual. A more general impression seems to be that children are intermediate between, a blend of, their parents. This impression, though true in fact, can be dangerously misleading. A character such as skin colour in human races suggests that the crossing of extreme types leads to blending, for the typical mulatto (offspring of a negro-white cross) is intermediate in skin colour. However, geneticists working in places where there is a good deal of interracial crossing have been profoundly impressed by facts of inheritance of a very different kind. An example from Lotzy's work, concerning a family in South Africa, may be quoted. A Griqua woman married a Scot, and they had a daughter who also married a " white " man. Four of the sons of this couple were described as very different in appearance. One was very tall, almost white, with brown eyes and frizzy hair ; another was of medium height, with a darker skin, brown eyes, and long straight black hair ; a third was of medium height, with a darker yellow skin than the second, brown eyes, and Kaffir-like hair ; the fourth was of medium height, of darker skin than the first mentioned, brown eyes, and brown-black Hottentot hair. Their features were very different. An example such as this—and there are very many which could be quoted—illustrates vividly the principle of *segregation* of characters. We see around us many examples of segregation, and comment on them in such words as, " Mary has her mother's eyes and her father's nose." Such facts suggest that, in some way, specific characters retain their identity and can be transmitted and distributed in different combinations or patterns in different individuals. Early attempts to formulate laws of heredity failed because investigators did not recognize the necessity for dealing with individual characters separately. The imaginary Mary, with her mother's eyes and her father's nose, and perhaps not strikingly like either mother or father in other respects, gives little if any clue to the laws of inheritance, but if one clear-cut and definite characteristic, such as eye colour alone, is taken and examined in various members of a family, and traced through ancestors, then we should have more chance of discovering the laws. Human beings, however, are not suitable material for the initial work on heredity with a view to establishment of laws. Other animals are better ; and it was in work with plants that the laws were discovered. Several workers on plant hybridization in the eighteenth and nineteenth centuries had realized the necessity for consideration of separate characters. It was Mendel's recognition of the single character as the unit, his determination to investigate these units, his doing so with long continued precise experiments, his setting forth of results with clarity, and above all his imagination in the interpretation of the results, that gave him the key to the laws of inheritance. Gregor Mendel, a monk living in Brno (at that time in Austria), carried out his experiments in the monastery garden, publishing the results of his work in a local journal in 1865. But it remained long neglected. Charles Darwin apparently never heard of it. It was not until the year 1900 that three other workers on heredity independently arrived at similar conclusions, and by searching for other literature on the subject discovered his work and confirmed his results by their own experiments. Since then an incredible amount of work has been done with these laws as a basis, work of profound significance for the lives of human beings. The principles, or laws, of inheritance which Mendel set forth, and which, together with subsequent work, have in posthumous recognition been called Mendelism, were founded on experimental facts. They can best be explained by reference first to his experiments and next to those of others. He chose for his experiments the common edible pea (*Pisum sativum*), of which there are several well-marked varieties, having definite, clearly differentiated characteristics. One variety is tall (6 ft.–7 ft.), another short or dwarf (9 in.–18 in.). In one variety the seeds are round, in another they are wrinkled ; the seed may be yellow or green ; the seed coat may be white or coloured ; the pods may be deeply constricted or simply inflated ; they may while unripe be green or bright yellow. It was these and other such contrasting pairs of characters that Mendel decided to investigate, at first taking each pair of characters separately. The importance of the consideration of separate character pairs cannot be overestimated ; in it lay the secret of Mendel's success. Taking a number of tall plants of a pure strain (*i.e.* one that had produced nothing but tall plants for generations) he crossed them with dwarfs, likewise of a pure strain. By " crossing " is meant that the pollen from the stamens of the flowers of the tall plants was placed on to the stigmas of the flowers of the dwarfs, or vice versa. It was found that the results were identical whichever way the cross was made. Each pollen grain grows into a pollen tube containing a male cell which, after the tube has grown down from the stigma into the ovary, unites with the egg cell within an ovule to form, after subsequent growth, a seed. Only one male cell can unite with one egg cell. The seeds thus formed were collected and sown and found to produce plants *all* of which were *tall.* When these plants (first filial generation) were inbred, that is either cross-fertilized among themselves or self-fertilized (*i.e.* pollen and ovule from the same flower), and the seeds sown, the dwarf type of plant reappeared. Consideration of large numbers showed that in this second generation after the original cross (second filial generation) the proportion of tall to dwarf plants was three to one, and *there were no intermediates or transitional types.* This does not mean that all the talls were equal, or all the dwarfs, but the variation was " discontinuous " in the sense that the shortest of the talls was taller than the tallest of the dwarfs : they remained two clearly distinguishable varieties. When the dwarf plants were inbred they gave in all succeeding generations nothing but dwarf plants. The talls, however, of this second filial generation when inbred gave in the next generation (*i.e.* the third filial generation) both tall and dwarf plants. While the dwarfs, as we have seen, bred true to dwarfness, the talls did not all behave alike. Approximately one-third of the talls of the second filial generation bred true to tallness and two-thirds gave tall and dwarf plants in the proportion of three to one. In every case dwarf plants, when inbred, continue to give only dwarfs in their progeny, whereas tall plants are of two kinds, some breeding true and others not. It cannot be predicted from the appearance of the tall plants which will breed true and which will not ; their nature is revealed by their offspring. Though all this may sound complicated, the facts can be represented in a diagram which may help to simplify the matter (see diagram 1). Some talls in the diagram are indicated as breeding true to tallness ; and for the sake of clarity of exposition they have always in each generation been placed to the left-hand side of the diagram. It must be remembered that although a certain proportion of talls breed true, we cannot tell by mere inspection which will do so. Dwarfs, on the other hand, can be recognized by their appearance, and in spite of their mixed ancestry can be counted on to breed true. The character of tallness, which appears to the exclusion of dwarfness in the first filial generation, Mendel called *dominant.* The character of dwarfness, which seems to remain latent and reappears in the offspring of the self-fertilized or the inbred hybrid in the second filial generation, he called *recessive.* Mendel and subsequent workers obtained similar results with many other contrasting pairs of characters in a variety of different plants and animals. In peas, for example, yellow seed colour is dominant over green, round seed over wrinkled, and green colour of the unripe pod over yellow. In guinea pigs, rough coat is dominant over smooth, and black coat dominant over white.

The explanation he offered seems so simple that one wonders why it was not thought of earlier, and why, when offered, it was not immediately recognized. That is true also of the doctrine of evolution by natural selection. These simple explanations, however, require not only the ability to design experiments, and great patience in the amassing and sifting of evidence, but that rare strange gift of scientific imagination. Seemingly simple explanations may not be merely simple inductions from facts ; a flash of genius is required to interpret the facts.

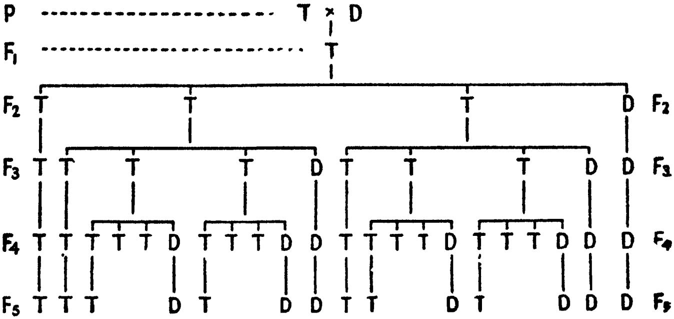
P T × D
F1 T
F2 T T T D F2
F3 T T T T D T T T D D F3
F4 T T T T T D T T T D D T T T T D T T T D D D F4
F5 T T T D T D D T T D T D D D F5

DIAGRAM 1

T = tall plant. **P** = parent generation.
D = dwarf plant. **F**$_1$, **F**$_2$, **F**$_3$, etc. = first, second, third, etc. filial generations.

NOTE.—This diagram could be extended indefinitely according to the plan.

To follow the explanation it must be remembered that the beginning of a new individual is the union of the male and female sex cells (or gametes). This is the only physical link between successive generations. In the crossing of the original tall and dwarf plants of pure stock the tall one may be considered to bear in the gamete (whether within pollen grain or ovule), and therefore to contribute to the union, some factor determining tallness.[1] A tall plant of pure stock has as far as tallness is concerned nothing but the factor for this character to give. Similarly the dwarf plant can only contribute a factor for dwarfness. The hybrid which is the result of the cross must be regarded as having a dual nature, bearing factors for both characters. Yet such an individual grows tall ; in some inexplicable way the factor for tallness expresses itself to the exclusion of the other. We must assume that this hybrid, in its turn, produces gametes bearing either factor but *never a combination of both* in one gamete. The factor must be considered as an entity, a unit which cannot be split. The members of a pair of factors separate one from the other in the production of the gametes—one factor going to one gamete, the other factor to another. This conception is fundamental. Large numbers of pollen grains and ovules are formed, and thus large numbers of gametes. In a hybrid presumably about half the pollen grains will bear the factor for tallness (let it be represented by T) and about half the factor for dwarfness (D), and similarly with the ovules. We cannot, however, tell by examining the pollen grains or ovules which factor they bear. A pollen grain bearing T will on the average meet an ovule bearing T as often as one bearing D, giving as the composition of all fertilized individuals either TT or DD, the numbers of which should theoretically be equal. Similarly a pollen grain bearing D has an equal chance of meeting an ovule bearing T or one bearing D, producing individuals TD and DD, with a 50 per cent chance of either, so that with large numbers we should expect equal numbers of each. Diagram 2 will serve to make this clearer.

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[1] This is not, it may be said, the character of tallness which is a character of the grown plant, but a determinant for this character.

As an analogy, imagine two boxes full of marbles, each containing equal numbers of black and white ones : using both hands and taking simultaneously a marble from each, sometimes we should get a black marble in each hand, sometimes a white in each hand, but more often there would come a black in one hand and a white in the other. If we did this simple experiment with large numbers, and put the categories mentioned into separate piles, we should probably find the pile of mixed black and white to be twice as large as each pile of black alone or white alone. This corresponds with the results of breeding experiments : the chance or random union of gametes may bring together those bearing the same factors or different factors. Naturally, if we experimented with only a few plants, the proportions 1 : 2 : 1 would not be at all certain to appear ; hence the necessity for experimenting with large numbers as did Mendel and others. Patience and skill in dealing with large numbers were certainly important factors in Mendel's success.

The term later given by Bateson to a contrasting pair of characters was "allelomorphic pair," each being the *allelomorph* of the other. The factors themselves are now spoken of as *genes*.

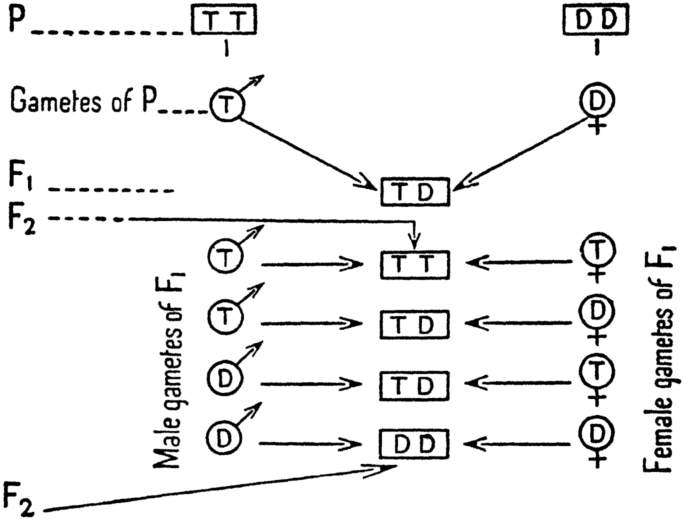

DIAGRAM 2

P = parent generation. F_1, F_2 = first, second filial generations.
The rectangles represent fertilized individuals, and the circles gametes.
♂ = male gamete. T = factor for tallness.
♀ = female gamete. D = factor for dwarfness.

Although the gametes of F_1 are produced in large numbers only four male and four female are represented for the sake of simplicity. They suffice to show the proportions. Although more pollen grains than ovules are produced they must unite in equal numbers, *i.e.* one pollen grain unites with one ovule. In F_2 $\boxed{\text{TT}}$ must necessarily breed true to tallness and $\boxed{\text{DD}}$ to dwarfness, whereas $\boxed{\text{TD}}$ will behave as does $\boxed{\text{TD}}$ of F_1. Here we have an explanation of Diagram 1.

The shorthand or symbol form which is generally used in diagrams is to designate the dominant factor by a capital letter and its recessive allelomorph by the corresponding small letter. Thus if " T " represents the factor for tallness in peas then dwarfness would be represented by " t." Using these symbols we can make

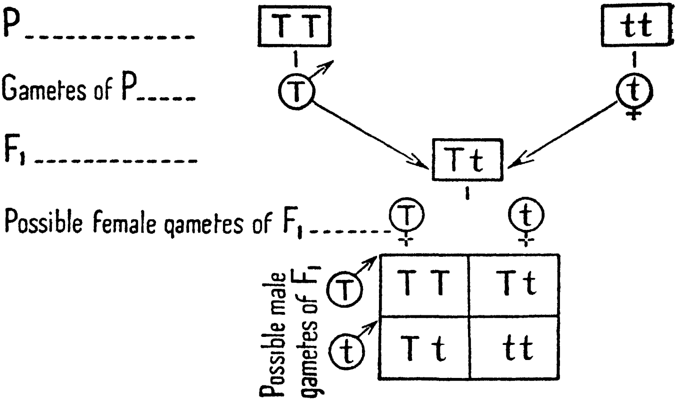

DIAGRAM 3

The checker-board shows the possible combinations of F_1 gametes to form the F_2 generation, in the proportions to be expected when large numbers are involved.

Compare Diagram 2.

another form of diagram 2—at least another diagram representing the same facts (see diagram 3). This diagram will facilitate the task of comparison when several pairs of characters have to be considered. It will be seen that the organism which develops from the fertilized egg (or zygote) has a dual nature. In respect of any given character it contains two factors—either identical, in which case the organism is said to be *homozygous* for that particular character, or dissimilar (*i.e.* the two different members of an allelomorphic pair), in which case the organism is *heterozygous* for that character. In the formation of gametes the factors, whether identical or dissimilar, separate : a gamete can contain one member of an allelomorphic pair, but not two. The gamete, unlike the zygote, has a single, not a dual nature. It is not possible, as has been said above,[1] for it to contain half of one gene and half of another. It is only on these assumptions—which, as we shall see in the next chapter, can be confirmed by microscopic observations—that the results of breeding experiments can be explained. A simple verification of the hypothesis consists in crossing a heterozygous individual, say of genetic composition Tt, with one of composition tt. The progeny expected would be 50 per cent tall and 50 per cent dwarf plants, because gamete " t " is equally likely to meet T or t, giving Tt and tt respectively. Breeding results are in fact in accordance with this expectation.

It is, however, impossible to conceive of even the simplest type of organism for which but one pair of characters, determined by one pair of genes, would be sufficient. In peas Mendel experimented with a number of characters, at first separately and then in combination. Let us consider two characters together and observe the result of crossing a tall pea plant having green pods with a dwarf one having yellow pods. All members of the first filial generation are tall with green pods. Large numbers reveal that when these are inbred the second filial generation consists of four different types, *viz.* tall plants with green pods, tall with yellow pods, dwarf with green pods, and dwarf with yellow ones, and the respective proportion is 9 : 3 : 3 : 1. Similar results are obtained with other allelomorphic pairs taken two together. How are they to be explained? The explanation offered by Mendel, and now with some modification universally accepted, assumes that in the formation of the gametes the different factors segregate *independently*. According to the notation already briefly explained the factorial (or genetic) composition of the original parent plants can be represented as TTGG and ttgg. Reference should now be made to diagram 4. This diagram, which corresponds to the results of breeding experiments on a sufficiently large scale, assumes the independent segregation of factors, and the checkerboard shows all possible combinations of the four possible kinds of F_1 gametes to form the F_2 generation. From the principles already enunciated it will be evident that the F_1 gametes could not possibly be Tt and Gg, because the members of an allelomorphic pair separate. If the diagram is examined it will be found that twelve of the combinations contain either one or two "T's," *i.e.* twelve plants are tall; this will readily be understood, as it has already been shown that the dominant character manifests itself both in the homozygous and the heterozygous state. Of these twelve talls nine have either one or two G's, and thus, for the reason just recalled, have green pods. Of the four combinations which represent dwarf plants, *i.e.* those containing two t's, three contain G and have thus green pods, and one contains two g's and has thus yellow pods. A summary of the diagram indicates $\frac{9}{16}$ tall green, $\frac{3}{16}$ tall yellow, $\frac{3}{16}$ dwarf green, and $\frac{1}{16}$ dwarf yellow. This is in agreement with the experimental facts: these

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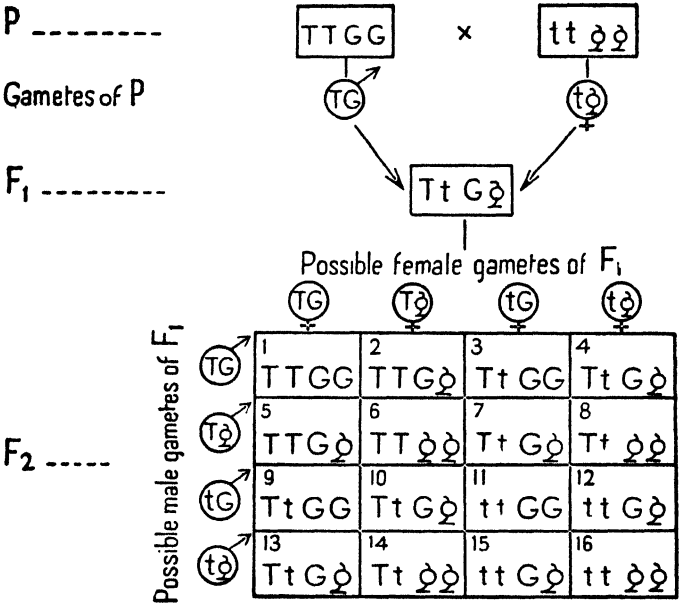
[1] See page 36.



	TG ♀	Tg ♀	tG ♀	tg ♀
TG ♂	1 TTGG	2 TTGg	3 TtGG	4 TtGg
Tg ♂	5 TTGg	6 TTgg	7 TtGg	8 Ttgg
tG ♂	9 TtGG	10 TtGg	11 ttGG	12 ttGg
tg ♂	13 TtGg	14 Ttgg	15 ttGg	16 ttgg

DIAGRAM 4

T = the factor for tallness and **t** the factor for dwarfness.
G = the factor for green pod and **g** the factor for yellow pod.
P = parent generation. F_1, F_2 = first, second filial generations.

Rectangles represent zygotes (*i.e.* fertilized individuals) and circles gametes.

The checker-board shows all possible combinations of F_1 gametes to form the F_2 generation, in the proportions to be expected when large numbers are involved.

Compare Diagram 3.

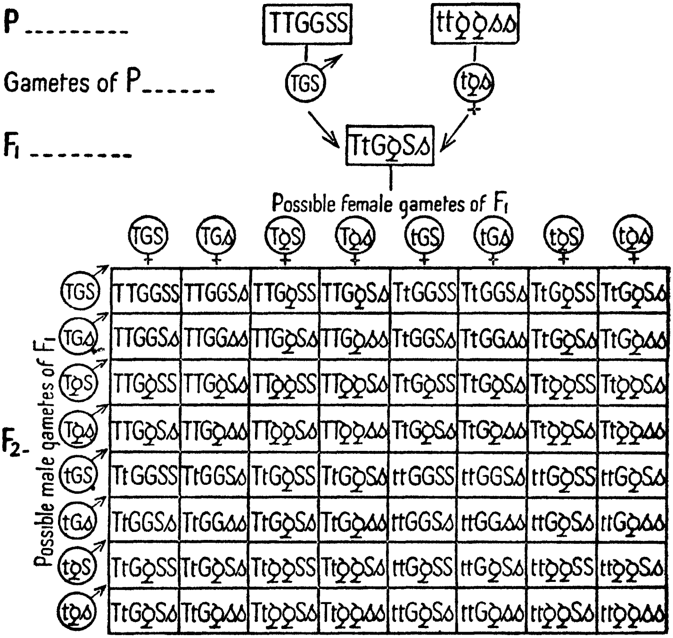
are the proportions actually obtained in breeding tests. The mathematical prediction agrees with the facts. The independent segregation of factors in the gametes is an established principle of Mendelism. Of the F_2 generation of peas just described, on the average only one in sixteen is genetically identical with each grandparent for the given characters, and the rest represent new combinations, of which the homozygotes TTgg and ttGG will, when inbred, breed true. If, however, the original cross had been between two plants of genetic composition TTgg and ttGG, the F_1 generation would necessarily be TtGg (formed by the union of the only possible gametes Tg and tG). Here is a close parallel to the case of Mary with her mother's eyes and her father's nose, for the F_1 generation, resulting from the crossing of tall yellow with dwarf green, is tall like one parent and has green pods like the other, these being the dominant characters. Agriculture has profited from a knowledge of Mendelism, and desirable characters can be combined by suitable hybridization. The new combinations of this nature provide some of the raw material of evolution, on which natural selection can work. Other kinds of change in constitution will be considered in Chapter III.

Let us briefly consider what happens when there are three pairs of factors involved. Take, for example, the three pea characters of tallness, green pod, and simple pod, which are allelomorphic and dominant to dwarfness, yellow pod, and constricted pod. Here all of the F_1 generation obtained on crossing tall, green, simple with dwarf, yellow, constricted resemble the former. Inbreeding of these in large numbers gives in the F_2 generation eight visibly different kinds in the following proportions :

$\frac{27}{64}$ tall, green simple pod.
$\frac{9}{64}$ tall, green constricted pod.
$\frac{9}{64}$ tall, yellow simple pod.
$\frac{3}{64}$ tall, yellow constricted pod.
$\frac{9}{64}$ dwarf, green simple pod.
$\frac{3}{64}$ dwarf, green constricted pod.
$\frac{3}{64}$ dwarf, yellow simple pod.
$\frac{1}{64}$ dwarf, yellow constricted pod.

Diagram 5 shows what would be expected on the assumption of independently assorting factors. If a count is made on this diagram of expectations, it will be found to agree with the facts just given. Convenient terms to remember at this stage are those used to distinguish between individuals which have the same factorial (genetic) composition and those which, though appearing alike, have not the same factorial composition. Factorial composition is called the *genotype*, and individuals of identical composition are described as *genotypes*. The appearance is called the *phenotype*, and individuals phenotypically alike are known as *phenotypes*, whether or not they are genotypes. Individuals may be phenotypes without being genotypes ; the reverse is clearly impossible. Sometimes factorial composition (genotype) can be inferred from ancestry. The offspring, for example, of a cross between TTGG and ttgg must be TtGg. We cannot usually determine genotype from phenotype alone, but can tell the difference only when the offspring are seen.

Referring to diagram 4—of the sixteen possible types in F_2, nine (viz. 1, 2, 3, 4, 5, 7, 9, 10, 13) are phenotypes, being tall with green pods, and of these Nos. 2 and 5 are also genotypes. There are other phenotypes and



	TGS	TGs	TgS	Tgs	tGS	tGs	tgS	tgs
TGS	TTGGSS	TTGGSs	TTGgSS	TTGgSs	TtGGSS	TtGGSs	TtGgSS	TtGgSs
TGs	TTGGSs	TTGGss	TTGgSs	TTGgss	TtGGSs	TtGGss	TtGgSs	TtGgss
TgS	TTGgSS	TTGgSs	TTggSS	TTggSs	TtGgSS	TtGgSs	TtggSS	TtggSs
Tgs	TTGgSs	TTGgss	TTggSs	TTggss	TtGgSs	TtGgss	TtggSs	Ttggss
tGS	TtGGSS	TtGGSs	TtGgSS	TtGgSs	ttGGSS	ttGGSs	ttGgSS	ttGgSs
tGs	TtGGSs	TtGGss	TtGgSs	TtGgss	ttGGSs	ttGGss	ttGgSs	ttGgss
tgS	TtGgSS	TtGgSs	TtggSS	TtggSs	ttGgSS	ttGgSs	ttggSS	ttggSs
tgs	TtGgSs	TtGgss	TtggSs	Ttggss	ttGgSs	ttGgss	ttggSs	ttggss

DIAGRAM 5

P = parent generation. **F$_1$**, **F$_2$** = first, second filial generations.
T = the factor for tallness and **t** the factor for dwarfness.
G = the factor for green pod and **g** the factor for yellow pod.
S = the factor for simple pod and **s** the factor for constricted pod.
Rectangles represent zygotes, and circles gametes.

The checker-board shows all possible combinations of **F$_1$** gametes to form the **F$_2$** generation, in the proportions to be expected when large numbers are involved.

genotypes which can be discovered by inspection. If diagram 5 is examined from the same point of view it can be seen that among the twenty-seven tall plants with green simple pods (*i.e.* phenotypes) the following genotypes are found: TTGGSS, TTGGSs, TTGgSS, TTGgSs, TtGGSS, TtGGSs, TtGgSS, TtGgSs. These diagrams will repay examination and reflection. From them we can see that with two independently assorting pairs of factors (diagram 4) there are four kinds of gametes produced by F_1 giving sixteen possible combinations in F_2, of which some are alike, leaving nine different genotypes. Those arranged on the diagonal line from top left to bottom right-hand corners are homozygous, two of them new combinations which will breed true. With three pairs of factors (diagram 5) there are eight kinds of F_1 gametes and sixty-four possible combinations in F_2, among which there are eight visibly different kinds (phenotypes), and twenty-seven different genotypes. With two-factor pairs only one in sixteen is likely to resemble either grandparent genotypically, with three-factor pairs only one in sixty-four. With four-factor pairs there are sixteen kinds of gametes in F_1, giving 256 possible combinations in F_2, among which there are sixteen different phenotypes and eighty-one different genotypes. Only one in 256 is likely to resemble either grandparent genotypically. Thus we see that the chances of identity with parents become very much more remote the greater the number of characters under consideration. This is merely a re-statement of common experience. Although we may frequently find a child with one or more parental features, who has ever seen a child the exact replica of the parent? One could, if patience would endure it, use the checker-board method of finding the number of possible combinations in F_2 with greater numbers of independently assorting factor pairs. In practice, however, it is much easier to resort to formulæ, for, with only ten independently assorting factor pairs involved, there is the chance that only one in 1,048,576 will genotypically resemble either grandparent, and we should spend a prodigious time demonstrating this graphically. There is no certainty that all the combinations indicated by the diagrams will be found. Very large numbers would have to be used in order to get anything like the proportions shown; they represent mathematical probability.

CHAPTER III

THE PHYSICAL BASIS OF INHERITANCE: CHROMOSOMES: MUTATION: THE INHERITANCE OF SEX

THE fundamental principles of segregation and of independent assortment of factors in the gametes were established by inference from the results of breeding experiments, and in a similar way was the hypothesis tested. Evidence amounting to proof was later forthcoming. As microscopes were improved, and as knowledge of cell structure and cell division increased, there were found within the cells certain structures called *chromosomes*, whose behaviour was found to be so closely parallel to the postulated behaviour of the determining factors as to leave no doubt that they were the bearers of the actual genes.

It seems desirable to give here a short account of the process of cell division. Leaving out of account some lower organisms and some irregularities, a plant or animal body, for example a human body, begins its life as a single cell, which itself results from the union of two gametes or sex cells representing the only physical link between successive generations. The sex cell produced by the female is the egg cell (or *ovum*) and that by the male animal the *spermatozoon*, and their union is termed fertilization. The fertilized egg cell divides into two cells which do not separate from each other; these cells increase in size and each divides into two, the products of division still remaining together. By successive divisions a small sphere of cells is formed, and eventually a large body, perhaps, as in the case of our own bodies, containing innumerable millions of cells. Whenever growth in a body is taking place cells are dividing into two. Growth is a process of cell division followed by increase in the size of the cells which are the products of division. A living cell arises from a pre-existing one. Certain stages of visible growth may, however, be the enlargement of cells previously produced by division. One of the amazing things about cell division is the accuracy of the process which ensures that the products of division are identical. Although a plant or animal body may ultimately be made up of many different kinds of cells, yet in the early stages of the organism's development all the cells appear similar, and only later is there gradual differentiation into different tissues and organs. There is no time here to consider various intrinsically interesting facts about the physiology of development, because that would take us from the immediate concern of cell division in relation to heredity.

The initial fertilized egg cell, or any cell capable of division, appears in the resting stage as a little mass of jelly-like substance of complex composition called *protoplasm*, bounded by a membrane, or in plants by a definite cell wall. The denser central part of the protoplasm is called the *nucleus* and the outer part the *cytoplasm*. The nucleus is the most important part of the cell and is the centre, or control, of the cell's activities. Its importance in heredity in comparison with that of the cytoplasm is suggested by facts already mentioned in connection with experiments on hybridization, namely, that reciprocal crosses give identical results. That is to say, it does not matter whether the dominant character is brought in by the egg cell or by the sperm. This implies that each parent contributes an equal amount to the offspring, even although the egg cell may be very many times larger than the sperm. The egg and sperm each contribute from their *nucleus* half the nucleus of the fertilized egg : the quantity of the cytoplasm does not affect the transaction. The nucleus, which is surrounded by a membrane, appears as a clear fluid in which is suspended a network (*reticulum*) of denser substance. This network, because it consists of material which easily stains with certain dyes, is called *chromatin* (from Greek *chroma*, colour). Prior to cell division, changes begin to appear in the cell. The nuclear reticulum appears as a thread which breaks up into several pieces, the *chromosomes*, each of which splits longitudinally into two equal parts. The nuclear membrane breaks down, and in the centre of the cell—in the space occupied by the nucleus—appear fibre-like structures in a spindle shape, *i.e.* converging at opposite poles. The chromosomes, each already split down the middle, are arranged along the centre or equatorial plane of the spindle. The halves of each chromosome now separate and appear to be attracted along the lines of the fibres to opposite poles of the spindle. There is thus aggregation at each pole of a set of chromosomes identical in number and kind to those of the original nucleus. The chromosomes now lose their identity, and each set becomes a new nuclear network surrounded by a nuclear membrane. The cytoplasm divides into two, and two new cells are now constituted. This kind of cell division is called *mitosis* (or mitotic cell division) (see diagram 6). Mitosis occurs in the first cleavage of the fertilized egg cell and in the subsequent innumerable cell divisions which occur in the building up of a plant or animal body, or in the renewal of tissues. The most noteworthy feature of the process is the exact longitudinal division of the chromosomes into halves, whereas there seems to be no mechanism for ensuring exactly equal division of the cytoplasm. This fact, and the equivalence of the unequal-sized egg and sperm as bearers of hereditary factors, early suggested that the nucleus rather than the rest of the cell was the receptacle of this hereditary material. A great deal of evidence confirms this view. There are, admittedly, cases in plants of cytoplasmic transmission—in fact, it is

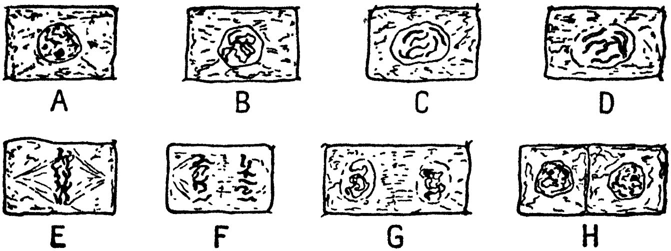


DIAGRAM 6

CELL DIVISION—MITOSIS

A, resting cell; the chromatin of the nucleus is a network. B, chromatin thread appears, and in C this has divided into chromosomes which in D are each split down the middle. E, the split chromosomes are arranged on the equatorial plane and have begun to separate. F, the half-chromosomes are drawn towards the poles—a complete set to each pole; in G they are arranged as a chromatin thread, and the beginning of a new cell wall has arisen, and in H two new cells each similar to A are constituted. There are six chromosomes (*i.e.* three pairs).

through the cytoplasm that the plastids containing colouring matter are transmitted, and there are a few disputed cases in animals. But these do not affect the general conclusion that the chromosomes are the bearers of the hereditary factors.

In any organism which grows from a fertilized egg the chromosomes occur in pairs (with an exception of great significance, which will be discussed later, pages 66ff). The members of each pair are alike in size and shape and are said to be homologous, but the members of one pair are visibly different in size and shape from those of other pairs. Apart from rare abnormalities, their number remains constant in every body cell of every individual of a species. From species to species, however, the numbers vary considerably. In man there are 24 pairs and in the hedgehog the same number; in the pig there are 20 pairs, in the horse 30 pairs, and in the vinegar fly (*Drosophila*) only 4 pairs. Although, when the nucleus is in the resting stage, the chromosomes seem to lose their identity, yet they appear at every cell division in the same numbers and with the same shape and size. All this forcibly suggests that there is continuity of the actual material embodied in the chromosomes throughout every cell of the body. Now one member of each homologous pair of chromosomes is derived from one parent and contributed by the ovum, and the other member is brought to the ovum at fertilization by the spermatozoon. Each gamete (whether ovum or spermatozoon) contains a single set of chromosomes, and thus half as many as a fertilized egg of the same species, or its derivatives by mitosis, which constitute the body cells of an individual.

We must briefly consider how this halving of the number of chromosomes is achieved. In the formation of gametes there occurs a different kind of cell division from that already described ; this is known as *meiosis*, or reduction-division. In plants it occurs at the formation of spores, and in animals in the sex glands immediately prior to the formation of the sex cells. In meiosis the chromosomes do not split longitudinally as in mitosis, but arrange themselves on the equatorial plane of the spindle in homologous pairs. Members of homologous pairs separate, going to opposite poles, there to constitute fresh nuclei, each having half the number of chromosomes of the body cells (see diagram 7). These two nuclei immediately divide by the ordinary mitotic process, *i.e.* without reduction, thus resulting in the formation of four cells each with half the number of chromosomes possessed by the body cells. In the male the four cells thus formed are all gametes ; spermatozoa are produced in groups of four. In the female organism only one becomes a mature egg (or ovum), and the three others, called polar bodies, are small degenerate cells. The difference in numbers produced would seem to be associated with size ; the ova, which are larger than the male cells and lack their power of movement, contain food supply, whereas the motile male cells consist of little more than a nucleus and a tail. Gametes are said to be *haploid*, *i.e.* having the *single* quota of chromosomes ; the fertilized cell and the cells of the body which grow from it are *diploid*, *i.e.* having the *double* number. This halving and doubling of the number of chromosomes goes on from generation to generation in a continuous cycle. The halving of the number of chromosomes is of great significance in inheritance. Their behaviour in reduction-division presents a striking parallel to the inferred behaviour of the genes postulated in explanation of the results of breeding experiments. In reduction-division there cannot, obviously, be the same perpetuation of identity of material which results from the longitudinal splitting of chromosomes in mitotic cell division. There is, instead, a separation of hereditary material. Reduction of chromosomes is the moment in the life cycle when there actually does take place the segregation of factors.

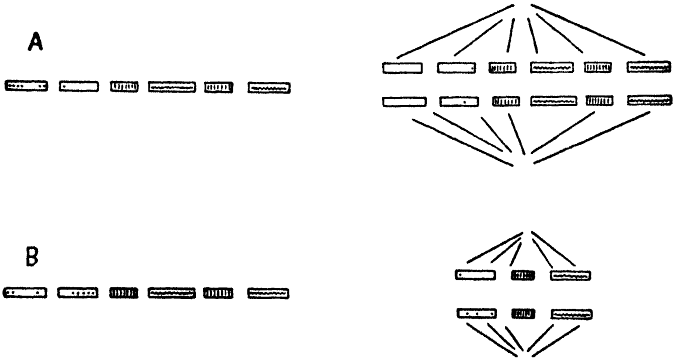


DIAGRAM 7

Diagrammatic representation of A mitotis and B meiosis. In the former each chromosome splits longitudinally, in the latter homologous chromosomes pair and then separate.

Imagine an organism whose body cells contain only two pairs of chromosomes, which, for convenience, can be labelled 1. 1a. 2. 2a., brought in originally by gametes bearing respectively 1. 2. and 1a. 2a. In the formation of gametes, 1. separates from 1a. and 2. from 2a., but they may not, at each reduction-division, be drawn to the opposite poles of the spindle in the same combination or in the original combination existing in the gametes before fertilization. They may, of course, happen to segregate in the original combination, or 1. may be associated with 2a., and 1a. with 2., at the opposite poles. Thus could be produced four kinds of gametes, viz. 1. 2.; 1a. 2a.; 1a. 2.; 1. 2a. There never occur together in one gamete 1. and 1a., or 2. and 2a.; always it can be observed that the members of homologous pairs separate. When these gametes unite with those similarly formed by the opposite sex it can be readily computed that there are nine possible combinations, viz.:

1. 1. 2. 2.	1. 1a. 2. 2.	1a. 1a. 2. 2.
1. 1. 2. 2a.	1. 1a. 2. 2a.	1a. 1a. 2. 2a.
1. 1. 2a. 2a.	1. 1a. 2a. 2a.	1a. 1a. 2a. 2a.

Some of these are more likely to occur than others, and by means of a checker-board diagram such as was used in the case of the hypothetical factors the probable proportions can readily be seen, and the situations are obviously identical (see diagram 8). The number of different combinations of chromosomes is the same as the number of genotypes in diagram 4. We can compute for any number of chromosome pairs the possible number of different gametes, remembering that members of homologous pairs separate; also the number of possible combinations of these gametes. As there are 24 pairs of chromosomes in man, a very large number of different combinations of gametes is possible (actually 3 multiplied by itself 24 times).

The parallelism between the behaviour of factors as postulated by Mendel and the behaviour of chromosomes as actually observed under the microscope should now be

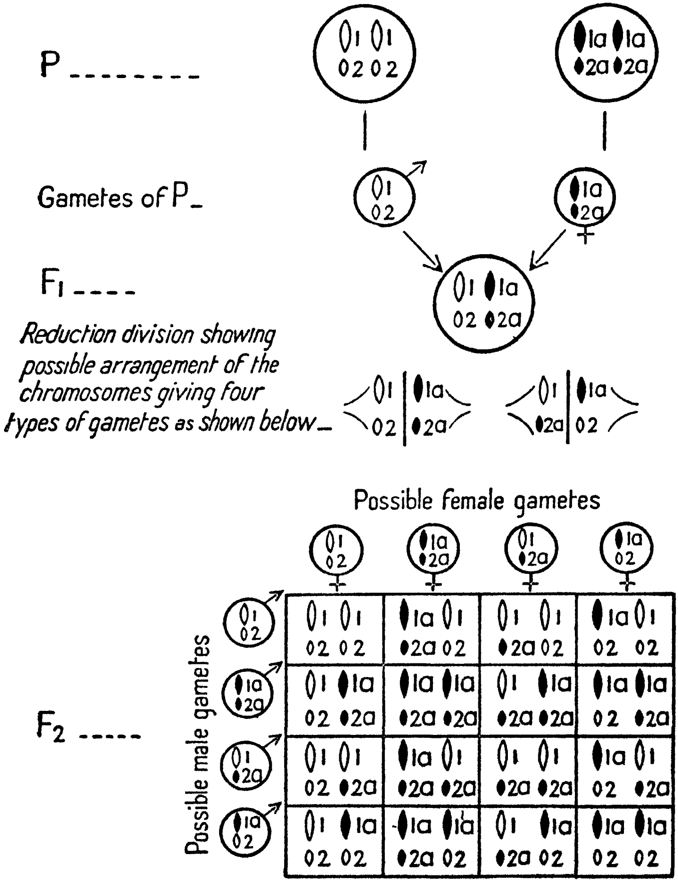

P
Gametes of P
F1
Reduction division showing possible arrangement of the chromosomes giving four types of gametes as shown below
Possible female gametes
Possible male gametes
F2
1
2
1a
2a

DIAGRAM 8

Diagram showing the independent assortment of two pairs of chromosomes, 1. 1*a*, 2. 2*a* (in F_1). The checker-board shows their possible combination to form the F_2 generation. Compare with Diagram 4.

P = parent generation. F_1, F_2 = first, second filial generations. As the size indicates, chromosomes 1 and 1*a* are homologous, as are 2 and 2*a*.

evident. The hypothesis and the observed facts agree. The chromosomes do occur in homologous pairs corresponding to the allelomorphic pairs of factors; the members of homologous pairs of chromosomes do separate from each other at gamete formation, just as it was postulated that the factors must segregate; moreover, the chromosomes retain their identity, as the factors were inferred to do in explanation of the reappearance of a character unaltered in generations following a cross. There is all this evidence and more to associate the factors with the chromosomes.

Are we then to assume that a chromosome is a factor? The answer is "No"—a factor cannot be a whole chromosome. In many species far more allelomorphic pairs of characters have been identified than there are chromosomes. In the fly *Drosophila*, which has for years been a subject of intensive study by Morgan and others, several hundred factor pairs have been identified, and yet there are only four pairs of chromosomes. Now experiment has shown that the principle of *independent* segregation of factors does not hold in all cases; certain factors, being *linked* in their inheritance, are presumably carried in the same chromosome. It was exceedingly fortunate that the early work of Mendel and others was concerned with characters which do segregate independently; otherwise it would have been practically impossible to discover the fundamental laws. The only way of explaining *linkage* is to assume that the chromosome is the bearer of many factors (genes). This is an assumption which has ample evidence to support it, and the genes are evidently arranged in an orderly manner along the length of a chromosome; which would necessitate the exact longitudinal splitting which has been described.

Chromosomes are seen under the microscope not to be of homogeneous consistency. Some parts stain more deeply than others and the outline is irregular. When stained, the appearance is rather similar to that of a link of beads. However, the visible portions which stand out from the rest (the " beads ") are evidently not the individual genes ; there are not enough of them ; they are too large and must represent many genes. Although the term " identification " of genes has been used, this does not mean that individual genes have been isolated and visibly recognized as such. They are known by the results they produce in the organism—" By their fruits ye shall know them." Similarly, in physics, the presence and structure of unseen atoms and molecules were inferred from their behaviour. There is no doubt of the reality of genes. A gene must be an actual amount of living matter, but a very small amount indeed. In *Drosophila*, for example, which has only four pairs of chromosomes, the inheritance of more than five hundred distinct characters has been traced to genes inherited according to Mendelian laws. Now a single cell of *Drosophila* is much too small to be seen except under a microscope ; yet in one cell there are four pairs of chromosomes comprising only part of the cell, and within the chromosomes are packed at least hundreds of genes. The term " gene " is, then, given to that minute part of a chromosome which exerts such a profound influence on the developing organism, determining and directing the development of its various characters. Although the gene has not been isolated, or even delimited from the rest of the chromosome, yet it can be assigned a *locus* or place in the chromosome relative to other genes. So much is known at the beginning of development ; and the later phases of the story, viz. the developed characters, can be seen and associated with different genes. Moreover, the way in which the genes exert their influences can in many cases be traced to some extent during the development of the organism, although initial phases remain obscure. Their manner of working is largely understood, for example, in the formation of various pigments. Some aspects of their action and interaction will be very briefly considered in the next chapter. Nuclear identity with cytoplasmic differences, and identity of genes throughout an organism composed of different parts, are the basic and somewhat paradoxical problems of development.

The existence and work of these minute genes may seem fantastic and inconceivable, but is it more inconceivable than the known fact that each one of us began life as a minute cell smaller than a pin-head? This cell is itself the union of ovum and sperm constituting the only tangible link between us and our parents, whose characters, however, we inherit. Biologists accept the chromosome theory of inheritance as the only possible explanation of the facts of inheritance as revealed both by breeding experiments and by the microscope. It is not a complete explanation, because, although it infers from ample evidence, and may be said to prove, that genes are parts of chromosomes, it does not explain how they work. However, biologists can increasingly explain biological phenomena in terms of chemistry and physics, giving scientific explanations to replace the older "vitalistic" and "animistic" ones, and the progress in knowledge of genes is remarkable. Much work on genetics is in progress in various parts of the world; when we consider what progress has been made in this science in less than forty years, there is hope that analysis of the work of genes will proceed until we know much more about their nature, manner of working, and possible control. A great deal of work has been done and instigated by Morgan, mainly on *Drosophila.* He has recognized four groups of characters corresponding to the four pairs of chromosomes, and even gone so far as to build up "chromosome maps" which indicate the relative positions on the chromosomes of hundreds of different genes. This has been done largely by the measurement of the strength of linkage. This requires a brief explanation. If two genes are located in the same chromosome we should expect them to remain together in all cases, and the characters determined by them to be always linked. This, however, is not the case ; linkage is found to be incomplete. Examination of chromosomes under the microscope gives a ready explanation of this. Just before reduction-division the members of each homologous pair of chromosomes lie very close together, sometimes adhering throughout their length, each portion of a chromosome apparently lying opposite to the corresponding portion of the other. Breakage and interchange of material apparently take place in such a way that part of one chromosome may join up with the opposite end-piece of its paired one (see diagram 9). Imagine the letters A,B,C,D. to represent homologous parts throughout the length of a chromosome and a,b,c,d. the corresponding parts in the other member of the homologous pair. Breakage and crossing over could give chromosomes A,B,c,d, and a,b,C,D, and others. Genes far apart are more likely to be separated than are those near together, *i.e.* a break in the chromosomes at *any* point would separate two genes situated at the extreme ends, whereas if two genes are located side by side only a break in one specific place can separate them. The interchange of parts of chromosomes is called *crossing over*. This interchange is sometimes further complicated by more than one break, resulting in *double crossing over*. Apart from rare instances of complete abnormalities, interchange occurs between corresponding parts of homologous chromosomes, *i.e.* between groups of allelomorphic genes. Allelomorphic pairs of genes thus remain in separate chromosomes in spite of crossing over. Linkage and crossing over are measurable phenomena, so that in spite of their complications order reigns in the knowledge accumulated. Recognition of linkage and crossing over has been the starting-point of fresh work.

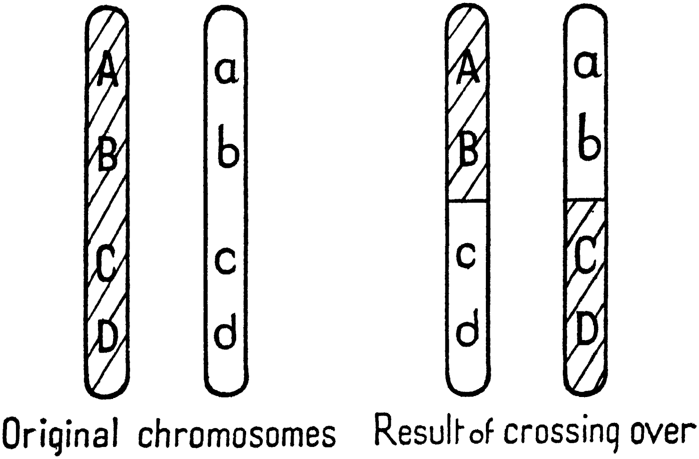


DIAGRAM 9

Diagram to illustrate the mechanism of crossing over between corresponding parts of homologous chromosomes.

Breakages in chromosomes are for experimental purposes actively induced by X-rays and radium. Gene location is sometimes determined by very direct evidence such as that furnished by Miss M'Clintock from maize; the absence of a measurable section in the length of a short chromosome has been found to correspond with certain abnormalities due to missing genes. Chromosome maps of other organisms are in progress. They are of great value in experimental work, and of great significance to all interested in the problems of heredity. They suggest the possibility of interference with the process of heredity, and a possible control of it, whose consequences are unpredictable.

Let us now consider for a moment the two aspects of heredity mentioned at the beginning of Chapter II., viz. segregation and blending. With a knowledge of the independent assortment of chromosomes which we have every reason to believe carry the genes, we can better understand the results of the breeding experiments described in Chapter I., and we can readily see an explanation of Mary's resemblance to her mother and father, and the typical segregation of characters in the family of the Griqua woman and the Scot described in Chapter II. In our experience we can no doubt think of many examples of segregation and of new assortment of characters in the offspring of a marriage. Examples of what would appear to be linkage are less common. Blue eyes with fair hair, brown eyes with dark hair are more frequent combinations than the reverse. The genes may be linked, and blue eyes with dark hair may be a case of crossing over; however, this is not certain. Although many cases of linkage can be cited in a variety of plants and animals, and even the amount of crossing over indicated, yet in man it is difficult to cite any definite cases except those of sex linkage, which will be discussed presently. Now, although the facts brought forward in this chapter help to explain segregation, there has not yet been offered any explanation of the fact of common experience, and, apparently, of contradictory nature, which was mentioned on page 30, viz., that the skin colour of mulattos is intermediate between those of their parents. Nothing so far considered would appear to explain this or a very large number of other phenomena of inheritance. However, these further complications, deferred for the moment, will be taken up in the next chapter.

Mutation

We must now consider the question of changes in hereditary material. Although fresh *combinations* of genes may provide some of the raw material of evolution, they obviously cannot provide it all, for progress would then be limited to possible combinations of already existing factors. Changes can take place in the actual hereditary material. In pure-bred stocks kept under uniform conditions a change may suddenly appear (one must know the stock to be sure that a new character is not a re-combination). For example, a race of red-eyed *Drosophila* was kept under uniform conditions for generations, and the red eye-colour was constant, until suddenly a white-eyed individual arose. This character being inherited, a white-eyed race could be produced. Such changes have been known among breeders of animals and plants for a long time as " sports." A change such as this can be shown to be due to a single gene, and the locus on the chromosome can in some cases be discovered. It is called a gene-mutation, or simply a *mutation*. It is a purely local change ; one gene may apparently change without those on either side, or even the allelomorph, being affected. A mutation may occur in body cells, cells producing gametes, or in the gametes themselves. If it occurs in body cells of animals it is not transferred to offspring, whereas in plants it may be, because the reproductive cells are formed late from the body cells. Moreover, vegetative reproduction may occur by cuttings, etc. If the mutation takes place in the gametes or in the cells producing them, it is handed on. Mutations seem to occur most frequently just prior to the formation of gametes. A new mutation behaves as a Mendelian factor. Most mutations are recessive—a good number produce undesirable traits. Some are lethal in the homozygous state (see page 80). The cause of the sudden appearance of mutations is unknown. A great deal of experimental work has been carried out with a view to bringing about mutation artificially. Müller showed more than ten years ago that X-rays increase the mutation rate in *Drosophila* about 150 times. It has been found that all types of short-wave radiations give rise to mutations : some of these mutations are those ordinarily found much less frequently, but others had not previously been seen in ordinary circumstances—presumably they had not been detected on account of their rare occurrence. Reverse mutation back to the original gene can also occur ; this, too, both normally and under the influence of X-rays. Gene mutations are rare. It is difficult to estimate their frequency except under controlled conditions of experiment with inbred organisms. New combinations of characters may arise on account of the bringing together of unsuspected recessives; and these could not, by mere inspection, be distinguished from the product of a mutation, unless the history preceding and following the appearance of the character were known. Several estimates of the frequency of mutations under laboratory conditions have been made, and the sudden appearance of a new gene is certainly a rarity. Out of about 30 million individuals of *Drosophila* bred in the laboratory there have been identified only about 500 gene mutations. Perhaps more occurred that were not identified; this would most probably be true of some of the lethal genes (see page 80). A suggested possible average is that a given gene might mutate perhaps in one individual in 500,000. As some genes tend to mutate more than others, it is extremely difficult to give anything approaching accurate figures. It is known that the same mutation occurs more than once; it probably occurs with a fairly definite measurable frequency. Different mutations may take place at the same locus on the chromosome, so that, instead of there being merely allelomorphic pairs of genes, there may be multiple allelomorphs, although no more than a pair (in relation to any one character) can occur in any one individual. Multiple allelomorphs can determine a graded series of differences in a character.

Although the amount of mutation ordinarily occurring is so very rare, it is too frequent to be explained solely by the amount of short-wave radiation generally and ordinarily occurring, so that, although the influence of short-wave radiations has elucidated some points about mutations, we are still left in ignorance of the normal causes of their occurrence. There is certainly no evidence that they are adaptations to the environment.

In addition to gene changes, heritable changes may sometimes take place by the breaking off of bits of chromosomes, the dropping out of whole chromosomes, or the addition of one by irregular segregation. Such phenomena are called *heteroploidy*. The number of chromosomes may be doubled, perhaps because of nuclear division without cell division; and other such phenomena collectively known as "ploidy" occur. They are more common in plants than in animals. Haploids also are found, where the egg develops without fertilization (known as *parthenogenesis*). This occurs in bees and wasps, and the eggs of frogs can be induced to develop parthenogenetically. None of these later mentioned phenomena of ploidy are known in man or other higher animals.

The Inheritance of Sex

It was stated on page 52 that in the diploid organism the chromosomes occur in pairs, but with one exception of great significance. We shall now consider this exception, which has led to the knowledge of sex determination by chromosomes. In most of the higher plants the same individual produces both male and female gametes, and all the chromosomes normally occur in pairs. In a few plants, and in most animals, the male and female gametes are produced by different individuals whose difference of function is associated with difference in form. The male individual (*i.e.* the one producing male sex cells or spermatozoa) is different in appearance from the female individual (*i.e.* the one producing female sex cells or ova), and in many types of animals there is a difference not only in form but in chromosome constitution. In some animals one sex has one more chromosome than the other has. It was discovered in the squash bug and in other animals that the female has eleven homologous pairs of chromosomes, whereas the male has ten homologous pairs and one odd chromosome. In reduction-division to form gametes, all the egg cells get eleven chromosomes, whereas in the formation of sperms some get eleven and others ten, *i.e.* they all get one member of each homologous pair, but only half can get the odd chromosome. An egg fertilized by a sperm containing eleven chromosomes will thus have eleven pairs of chromosomes and be a female, whereas an egg fertilized by a sperm with ten chromosomes will have ten pairs and one odd chromosomes and thus be a male. The odd chromosome is called the *sex chromosome*, because it, apparently, determines the sex of the individual which receives it (for convenient brevity it is called the x chromosome). Other chromosomes are termed *autosomes*. The position with regard to the squash bug can be summarized thus :

Female : 10 pairs autosomes + 2 x chromosomes
(10 A + 10 A + x + x).
Male : 10 pairs autosomes + 1 x chromosome
(10 A + 10 A + x).

In some plants, and in many animals, males and females have been found to differ not in the *number* of chromosomes but in the unequal *size* of one pair. In addition to the pairs of autosomes, one sex has two x chromosomes while the opposite sex has an x chromosome and a differently shaped, usually smaller, one called the y chromosome. In *Drosophila*, for example, the female has four homologous pairs of chromosomes, while the male has three homologous pairs and a pair of unequal-sized ones. One of these chromosomes is rod-shaped, as are the x chromosomes of the female , and the other, a y chromosome, is hook-shaped. The facts can be summarized thus :

Female : 3 pairs autosomes + 2 x chromosomes
(3 A + 3 A + x + x).
Male : 3 pairs autosomes + 1 x chromosome + 1 y chromosome
(3 A + 3 A + x + y).

As for the gametes, there are two kinds of sperms, viz. 3 A + x and 3 A + y, but all the ova have 3 A + x chromosomes. An ovum fertilized by a sperm of chromosome complement 3 A + y becomes a male individual (3 A + 3 A + x + y) ; one fertilized by a sperm 3 A + x becomes a female (3 A + 3 A + x + x).

Humans and other mammals have this "x y" type of sex determination. A woman has 24 pairs of chromosomes (*i.e.* 23 pairs of autosomes and 2 x chromosomes) in her body cells, and a man has 23 pairs of autosomes plus an x chromosome and a y chromosome. Our sex then is determined at conception (fertilization). Now the two kinds of sperms are formed in equal numbers, and it might be expected that an ovum would be equally likely to be fertilized by either kind of sperm. In human beings, however, the male determining sperm (23 A + y) seems to have some advantage over the other one in effecting fertilization ; it may be lighter and travel quicker. Whatever the nature of the advantage is, it results in there being a greater number of males than females conceived. Hence, although there are more deaths of male embryos than of female, the preponderance of males remains, and there are more boys born than girls. The infant mortality rate is higher for boys than for girls, and so the proportion of males to females falls. Actually the proportion of males to females falls throughout life, apart from a period during middle age, and there are more old women than old men. Insurance companies make a woman pay for the greater expectation of life by giving a smaller annuity for the same premium. Among some primitive peoples the proportion of males to females is, on the contrary, very high. The cause is not known—it is not explained by female infanticide. One reason for the greater mortality rate in males would appear to be the presence of male sex-linked lethal and semi-lethal genes (see Chapter IV.). A sex-linked gene is one carried in the sex chromosome (x chromosome). If a gene of a recessive character is carried in the x chromosome, the character will not be developed in the female unless she is homozygous for the character (*i.e.* carries two recessive genes), whereas in the male the character may show if only one gene is present in this x chromosome, apparently because the y chromosome is deficient in genes and does not carry the dominant allelomorph which could lead to the development of a character masking the effect of the recessive. The y chromosome does carry a number of genes, however, and it is known to carry genes not found in the x chromosome, resulting for some characters in a direct male to male inheritance of a character never found in females. A peculiar abnormal condition in man known as " webbed toes " is inherited in this manner. The first case of sex-linked inheritance was discovered in *Drosophila.* The eye colour of the wild type is red. A white-eyed male occurred as a mutation. On crossing with a red-eyed female all the F_1 were red-eyed (*i.e.* red eye is dominant to white).

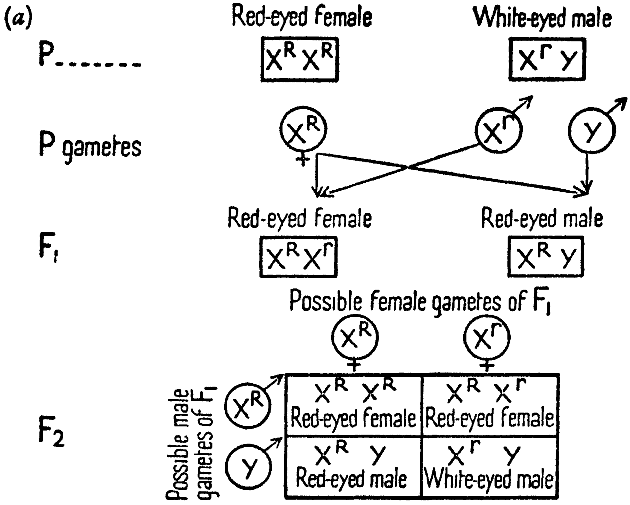


Diagram 10

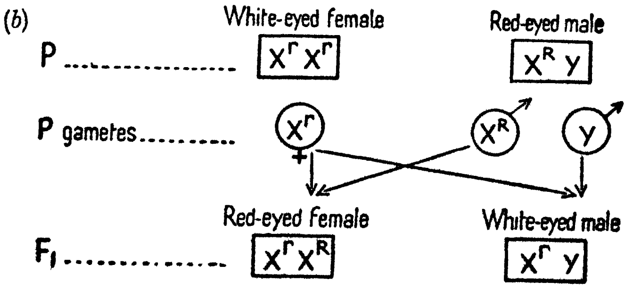
INHERITANCE OF EYE COLOUR IN DROSOPHILA

Each gamete has three autosomes in addition to the **X** or **Y** chromosome shown in the diagram. Each fertilized cell (and its derivatives by mitosis) contains three pairs of autosomes in addition to the **X Y** chromosomes.

R = factor for red eye (dominant).

For **P**, F_1, F_2, see Diagram 2.

r = factor for white eye (recessive).



Inbreeding gives an F_2 generation with the expected 3 : 1 of reds to whites, but, whereas all the females were red, only half the males were, *i.e.* the ¼ white of this generation were all male. In the next generation there are white-eyed females. It was then found that on crossing a white-eyed female with a red-eyed male all the female offspring are red-eyed and all the male white-eyed. These results can be explained if we assume that the gene for eye-colour is in the x chromosome (see diagram 10). The male cannot give the white eye-colour to male offspring because his contribution to that offspring is his y chromosome, which determines maleness in the offspring but does not bear the gene for white eye-colour. He gives his x chromosome bearing the gene for white eye-colour to his female offspring, who do not appear white-eyed as they have the allelomorphic gene for red eye-colour carried in the other x chromosome. This female can hand on this x chromosome bearing the gene for white eye-colour and can thus have white-eyed male offspring. In a similar way in human pedigrees a man may hand on a sex-linked character such as colour-blindness through his daughter, in whom it is not apparent, to his daughter's sons. (See Chapter V. for further consideration of this question.)

CHAPTER IV

MORE MENDELISM

THE principles of Mendelism described in Chapter II., although perhaps arithmetically complicated, are comparatively straightforward and simple. The account in Chapter III. of the correspondence in behaviour between the postulated factors and the actual chromosomes seen under the microscope serves to simplify the problem, although the process observed is itself complicated. Chromosomes are visible with the aid of the microscope. Of the genes we can only form a mental image, realizing that they are parts of the chromosomes. Many common phenomena of inheritance can be simply explained by the basic Mendelian laws, but there remain numerous facts for which the laws so far enunciated give no explanation alone. While the fundamental Mendelian laws remain as a sure foundation, there is built upon them a superstructure with innumerable complications.

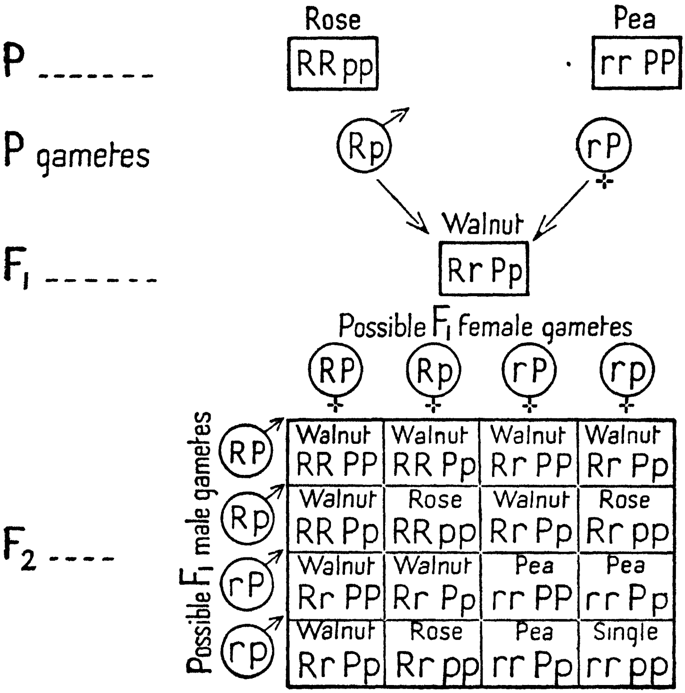
Incomplete Dominance

Complete dominance of characters is not a universal phenomenon. An early discovered instance of incomplete dominance solved a problem which had long confronted breeders of fowls. It had been found impossible to obtain blue Andalusian fowls which would breed true. It was then discovered that the blue Andalusian is the hybrid form obtained by crossing black with splashed white, and, of course, hybrids, being heterozygous, do not breed true. Blue Andalusians when inbred give 25 per cent black (*i.e.* homozygous dominant), 25 per cent splashed white (homozygous recessive), and 50 per cent blue Andalusian (heterozygous). The black fowls and the splashed white ones always breed true, the blue Andalusian never. This is comparable with the F_2 generation of peas ; 25 per cent homozygous recessive (dwarf), 25 per cent homozygous dominant (tall), and 50 per cent heterozygous, indistinguishable in appearance from the homozygous tall plants. In the fowls, however, heterozygous individuals differ in appearance from either of the homozygous types. Similarly, although in peas red flower-colour is completely dominant over white, this is not true of snapdragons. On crossing red-flowered with white-flowered snapdragons pink flowers are obtained. The red colour is incompletely dominant over the white, the heterozygous conditions giving the intermediate colour of pink. When these are inbred, red and white ones as well as pink appear in the next generation in the proportion of 1.1.2. Many other examples of incomplete dominance could be cited ; it must be a common phenomenon. No sharp distinction between complete and incomplete dominance can be established. Perhaps inability to discern differences allows us often to consider as indistinguishable in appearance the heterozygous and the homozygous forms, and in many cases it would be of great advantage to be able to distinguish between them. Obviously it would be advantageous to plant and animal breeders, and in the case of human beings it would be most useful, were some difference observable, to be able to say whether or not a person was heterozygous for a given trait, *i.e.* whether or not he or she carried a given recessive gene. It was indeed fortunate that the original characters investigated by Mendel showed " complete " dominance. This gave a simple key to the laws. However, it probably gave the impression that complete dominance was usual, and incomplete dominance rarer, which is probably not the case. The phenomenon of incomplete dominance can explain many cases of " blending " inheritance (*i.e.* characters of the offspring intermediate between the characters of the parents). It cannot, however, explain all. It does not, for example, explain the facts of the inheritance of human stature, which will be considered in Chapter VI.

Interaction of Factors: Complementary Factors

The phenomenon of incomplete dominance shows that the genes do not really work out an independent destiny. Although remaining independent units they can produce different effects in co-operation, and many complexities result. There are innumerable examples of this phenomenon of interaction of inheritance of factors. The classic example of comb shape in fowls may be quoted. It concerns the four types of comb shape, viz. rose, pea, walnut, and single. When fowls with pea-shaped combs and those with rose-shaped are crossed, the offspring all have walnut combs. When inbred these give $\frac{9}{16}$ walnut, $\frac{3}{16}$ rose, $\frac{3}{16}$ pea, and $\frac{1}{16}$ single-combed birds. These proportions are the same as those obtained with two independently assorting factor pairs, and the explanation of the phenomenon appears to be that two pairs of factors are involved. These can be called R and P. The homozygous rose-combed bird can be represented thus, RRpp; and the homozygous pea-combed one, rrPP. On crossing rose with pea the genetic composition RrPp must be obtained, and this corresponds with walnut combs. The proportions and kinds obtained on inbreeding the birds with walnut comb are explained when it is recognized that the factor R (in either homozygous or heterozygous condition) without P gives rose combs, the factor P without R gives pea combs, while together they give walnut combs; and the single comb results from the presence (in the homozygous state) of both recessives, *i.e.* rrpp. (See diagram 11.)

The colour of sweet-pea flowers furnishes another example of the interaction of factors. The wild type from which a number of true-breeding cultivated varieties are descended has a flower mainly purple, but with red side-petals. Purple is dominant over white, and white types, as we should expect, usually breed true. However, on crossing some white varieties, flowers similar to the wild type were obtained. These, when inbred, gave $\frac{9}{16}$ purple (wild type) and $\frac{7}{16}$ white flowers. All the whites bred true but the purples behaved differently, some breeding true, others not. The explanation is that the colour of the wild purple flower depends on the presence and interaction of two pairs of genes. For flower colour the genetic composition can be represented as CCPP. Purple is obtained when both C and P are present, even in the heterozygous state. In the absence of either the flower is white, and white-flowered plants could have arisen—by mutation and subsequent crossing—of composition CCpp or ccPP. On crossing two such



	RP ♀	Rp ♀	rP ♀	rp ♀
RP ♂	Walnut RR PP	Walnut RR Pp	Walnut Rr PP	Walnut Rr Pp
Rp ♂	Walnut RR Pp	Rose RR pp	Walnut Rr Pp	Rose Rr pp
rP ♂	Walnut Rr PP	Walnut Rr Pp	Pea rr PP	Pea rr Pp
rp ♂	Walnut Rr Pp	Rose Rr pp	Pea rr Pp	Single rr pp

DIAGRAM II

INHERITANCE OF COMB SHAPE IN FOWLS

Diagram showing the interaction of factors for comb shape in fowls.

When both **R** and **P** are present the comb is walnut.
When **R** is present but not **P** the comb is rose.
When **P** is present but not **R** the comb is pea.
When neither **R** nor **P** is present the comb is single.

white-flowered plants the composition CcPp is obtained, which, having both C and P, is purple. Factors co-operating in the production of a character, as in flower olour of sweet-pea, are called *complementary factors.* It as been found by chemical analysis in sweet-pea plants nd others that, where white races on crossing give oloured flowers, each race contains a different essential omponent of a pigment (colouring matter). The olour can actually be obtained by mixing extracts of hese two components obtained from the plants. There s then in this instance some indication of how complementary factors work.

Here is another instance. Crosses between different trains of "fancy" varieties of mice give the greyish brown colour of the wild mouse, and several factor pairs re involved. "Reversion to type," once a mysterious henomenon, is thus explained in terms of complemen-ary factors. Numerous cases of interaction of factors re known, some of them of a very complicated nature.

Multiple Factors

Experimental work by Nilsson-Ehle on the colour of wheat grains is of great importance in the question of lending inheritance. The red colour of some varieties s incompletely dominant over the white colour of others. The offspring of red and white are not such a dark red as he dark parent. In the F_2 generation following a cross f some varieties there are $\frac{3}{4}$ red to $\frac{1}{4}$ white, after other rosses $\frac{15}{16}$ red and $\frac{1}{16}$ white, while in other cases $\frac{63}{64}$ red o $\frac{1}{64}$ white are obtained. Breeding tests indicate that ne, two, or three factor pairs respectively are involved.

Diagram 12 represents the state of affairs when two factor pairs (R_1, r_1, R_2, r_2) are concerned. The presence of one factor for red (R_1 or R_2) is sufficient to cause red colour, but the colour is progressively more intense with two, three, or four factors present. The great importance of this case lies in the fact that the effect of the factors determining colour is cumulative. Such factors which are cumulative in their effect are called *multiple factors.* The conception of multiple factors is of extreme importance for an appreciation of the inheritance of quantitative characters (*e.g.* size characters—where there is continuous variation, as in human stature—as distinct from peas, where there are either talls or dwarfs). It can give an explanation of the kind of blending inheritance that is found, for example, in the skin colour of mulattos. The range of height or of colour respectively is undoubtedly a matter of the number of dominant or recessive genes present. Fundamentally the mode of inheritance can be interpreted according to Mendelian principles. The ultimate units of inheritance in the genes obey the Mendelian laws, but a character depends on the cumulative effect of many genes, and its intensity depends on the number of factors present. In the case of the wheat described above analysis could be made and the number of factors involved determined. This is frequently impossible (the character may defy analysis and Mendelian methods are not possible) and another method of estimating intensity of inheritance is resorted to. This will be described in Chapter VI. Not every definable character of an organism can be assigned to a gene which causes it, or even to several interacting genes. Although it seems certain that all characters are determined by genes working out their effects under environmental conditions,

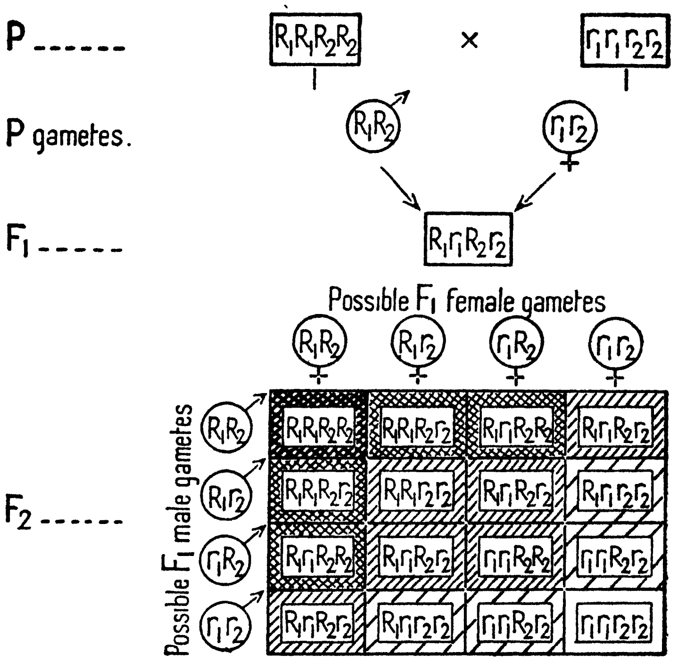


DIAGRAM 12

COLOUR INHERITANCE IN WHEAT GRAINS

Diagram showing the result of a cross between red- and white-grained wheat. The colour is progressively more intense according to the presence of 1, 2, 3, or 4 dominant factors (**R_1** and **R_2**). See page 77ff.

For **P**, **F_1**, **F_2** see Diagram 4.

we cannot look at an individual, analyse it into all its component elemental characters, and discover the determining genes, saying whether they are dominant or recessive.

Multiple effects of Single Genes: Ductless Glands

It has been shown that a character may be due to the interaction of several genes. It is necessary to emphasize that each gene does not affect only one character of an organism, or produce but one specific effect. It is common to speak of the gene for blue eyes or the gene for flower colour. But such genes, being present from the beginning of the organism's existence, probably produce other less obvious effects. Mendel noticed that plants bearing coloured flowers had also a slightly reddish colour at the base of the leaves. In such a case as this only extensive experiment might prove whether or not the phenomenon was due to linkage or to the general effect of a single gene. In the example quoted the evidence indicates that the colour of the leaf bases and that of the flower are due to the effect of a single gene. There are numerous instances of the multiple effects of a single gene, which may often have a profound effect on the whole organism. Some genes, indeed, produce such extreme modification of the whole organism that beyond a certain point development is checked and death ensues. Such a destructive factor is said to be *lethal*; a number are known in various plants and animals. They are all apparently of recessive nature, having effect only in the homozygous state, and being carried with impunity in the heterozygous state. In some cases their specific effect can be observed, in others only the final result, *i.e.* death, is seen and the mode of operation remains obscure. No sharp line can be drawn between lethal factors and others whose effect, though not fatal, may be gravely deleterious. An interesting case may be cited, viz. the inheritance of stunted growth in house mice. In strains possessing the gene dwarf mice appear among the offspring of heterozygous parents in the proportion of 1 dwarfed to 3 normal, indicating a character dependent on one gene. The dwarfed ones stop growing when about a fortnight old and achieve only about a third of the size of their fellows; moreover, they are sterile. Examination reveals that there is a deficiency of the pituitary gland, which affects the growth of the whole body, and of the adrenal gland. Treatment by implanting pituitary gland from rats results in development almost to normal size, and in males may lead to fertility. The supply of gland artificially given can largely neutralize the effect of the gene. We have some idea, then, how extensive is the work of this gene. This case shows the far-reaching effects on the organism of the secretions of the ductless glands. In recent years a great deal has been heard of these ductless or endocrine glands which discharge into the bloodstream directly (*i.e.* not through a duct) minute quantities of substances called hormones. The chief of these glands are:

The thyroid gland—situated in the neck astride the trachea.
The parathyroids—four small glands close to the thyroids.
The pituitary—a small organ with two lobes, anterior and posterior, situated near the base of the skull.
The pineal body—a small organ about the size of a pea, near the brain.
The "islets of Langerhans" in the pancreas.
The suprarenals—near the kidneys.
The interstitial tissue of the gonads (reproductive organs).

The different substances secreted by the glands are called hormones. These have a profound effect on the body and mind, and any derangement of the functions of the glands which upsets the balance of hormones may have very serious consequences. The thyroid gland plays an important part in development. In humans, cretinism, a type of deficient mentality associated with peculiar and severely arrested physical development, is due to failure of development of the thyroid gland. The condition can be somewhat alleviated if thyroid extract is taken early enough and always continued. A form of dwarfing in men and other animals, called *achondroplasia*, is due to derangement of the thyroid gland, and is inherited. Some people have excess of thyroid and are exceedingly active, wearing themselves away at too great a rate. In extreme cases part of the thyroid gland is removed by a surgical operation. A deficiency of thyroid leads to lethargy, low pulse, and slower rate of living, dry thick skin, poor growth of hair, dull and sleepy-looking eyes, and probably dull personality. Some " slimming " preparations contain extract of thyroid glands which increases the rate of living and " burns up " superfluous fat. The indiscriminate use of such preparations is undesirable and, to those with weak hearts, positively dangerous.

The fact that the thyroid gland affects both skin and hair characters is of great interest, as these are important characteristics used in the classification of human races. Moreover, the thyroid gland appears to affect the development of the skeleton. Arthur Keith has shown that thyroid deficiency causes arrested development of the base of the skull. The top of the nose becomes flattened, appearing as if drawn back between the eyes, the upper forehead bulges, and the face is somewhat flattened. These are to some extent Mongoloid features, and to a lesser extent Negroid ones. Differences in gland activity have probably been factors in determining races.

The effect of the thyroid on hair is well shown in sheep, where administration of thyroid extract can improve the quality of the wool. Its effect on growth is illustrated by experiments on amphibians. Tadpoles fed on thyroid gland extract quickly develop into frogs, even though very small ones, long before the proper time for their change of form. Tadpoles deprived of their own thyroid go on growing but never become frogs. The Mexican axolotl—a newt-like animal having both lungs and gills—will not normally change this state, but if injected with thyroid for a period it will lose its gills and become a solely air-breathing animal.

Of the parathyroids less is known, but they appear to control the calcium metabolism of the body.

The pituitary gland, like the thyroid, is concerned with development. The posterior lobe seems to be concerned with activation of muscles ; the anterior lobe has many functions, including some control of the achievement of sexual maturity. Experiment has shown that young salamanders fed on an extract of the anterior lobe become giants. Conversely, if this lobe is removed, the animal never grows up, but remains dwarfed and stunted. Dwarfs in cattle are associated with lack of pituitary anterior lobe. *Achondroplasia*, the form of dwarfing already mentioned, is associated not only with lack of thyroid but also with lack of pituitary anterior lobe. Giants may owe their development to excessive pituitary gland ; and a defect called *acromegaly*, in which there is an enlargement of the flesh and the bones of the face, hands, and feet, is due to an enlargement of the pituitary gland.

The so-called islets of Langerhans in the pancreas are certain areas secreting the hormone insulin on which much work has been done and much has been written in recent years. Insulin is concerned with the digestion of sugar into a form suitable for various organs to use, and lack of insulin causes the disease *diabetes mellitus*. Insulin treatment can give relief to diabetics.

The suprarenal glands lying on the front edge of the kidneys are closely connected with the nervous system. Their effect is prompt and of a temporary nature. Adrenalin secreted in the blood keeps up blood pressure and preserves muscular and nervous tone. Experiments on animals show that the injection of adrenalin into the blood stream produces the symptoms associated with preparedness for immediate action. Addison's disease is a pathological condition of the suprarenal tissue. One of its symptoms in white races is a darkening of the skin due to a deposition of pigment, closely resembling the process of pigment-deposition in coloured races. Some control of human skin-colour is, then, associated with adrenal glands. This provides further evidence for the interesting theories of Arthur Keith on the differentiation of racial types according to the endocrine gland secretions.

The secretions of the interstitial tissue of the gonads—the sex hormones—have a profound effect on development, and lead to the production of the secondary sex characters which distinguish in appearance one sex from the other. A great deal of work on this subject has been done by Crewe and others. We have seen in the last chapter that sex is determined by the genes borne in the chromosomes. The male and female individuals secrete different hormones which produce characters associated with maleness and femaleness. Deterioration of sex glands leads to changes. The castrated male animal differs in form and temperament from the normal. Hens and ducks may change their plumage to that of cocks and drakes if their ovaries are removed. A capon (castrated cock) can be made to behave like a normal one if a piece of cock's testis is grafted into the body cavity. This shows the result of glandular activity (operating through the blood stream). Normal reproduction, however, cannot ensue because there is no possibility of connection between the reproductive ducts and the ingrafted tissue. "Sex reversal" can, therefore, be largely explained by hormones. We need not attribute it to witchcraft, as was done in the fifteenth century, when a "cock" which laid an egg was sentenced and burned at the stake. In sex reversal the chromosomes remain unchanged. A hen which develops cock characters retains the female's number of chromosomes, and vice versa.

This apparent digression on the subject of the endocrine glands is relevant to our subject—and of vast importance. The fact mentioned on page 81 that the malfunctioning of the pituitary gland in the mouse is dependent on a single gene proves that characters of the endocrine glands are inherited. There is other evidence—some from human beings—that the degree of development of the glands, and consequently of the amount of their secretions, is by nature hereditary. In human beings, however, we do not know of any gland abnormalities dependent on a single gene. The hormones secreted by the ductless glands can so effectively influence the body and mind that the problems relating to the mode of inheritance of their abnormalities and degrees of development are of the utmost importance. (See also Chapter VII.)

The case of the mouse with pituitary deficiency (page 81) shows that the effect of hereditary deficiency can be alleviated by treatment involving the restoration of the appropriate hormone. There is abundance of such evidence from human beings in the case of glandular and other defects. Such environmental influences (including medical treatment) as alleviate the individual's condition do not affect the inheritance, *i.e.* the chromosomes. A child could inherit gland defect from its parent whether the parent was " cured " or not. The child does not inherit the biological effects of the parents' environment. We shall return to this aspect of inheritance in Chapter IX.

Dependence of Genes on the Environment

We must not suppose that genes work out their effect independently of environment. Their expression is determined, or limited, both by the external environment and by the internal environment, which is itself determined by other genes. Obviously the original cell from which a plant or animal grows needs an environment in which to grow. Life consists of a dynamic relationship between organism and environment—synthesis of food from external sources, oxidation of carbon compounds using oxygen from the atmosphere to supply energy. An organism without an environment is inconceivable. No character can be due wholly to heredity or wholly to environment. Every character is dependent on the environment for its production—the same genes will behave differently under different conditions. In *some* cases no known difference of environment affects the course of development of genes in a living organism. For example, no known environmental influence alters the development of the peculiar anatomical abnormality known as *Brachydactyly* (short fingers) but some such influence may ultimately be found. A character is commonly spoken of as hereditary when no known range of environment alters the expected development of the character. A character is commonly spoken of as being due to the environment when it exhibits variations consequent on changes in the environment; but it must not be forgotten that any "environmental" character is also hereditary, as it results from the response of a certain inherited constitution to a particular environment.

In the Himalayan rabbit the eyes are pink, and the fur is normally white on the body, and black on the ears, feet, and tail; this is the *hereditary pattern* of the variety that obtains under normal conditions of environment. If fur is plucked from the white parts, white fur normally grows again there, but if the animal is placed in the cold (there is a definite critical temperature) while the new fur is growing, it will grow black. Likewise, if fur is plucked from the black parts, black fur normally replaces it, but if the part is kept warm—for example, by bandaging—the fur grows white. Evidently, then, what is inherited in the Himalayan rabbit is not a definite colour pattern, but a tendency to form pigment or not to do so according to conditions of temperature. The environment to which the animal is generally subject is such that the familiar or so-called hereditary pattern results ; but this pattern is due both to heredity and to environment. In discussion of inheritance we may talk of the inheritance of a developed character; but, strictly speaking, all that is inherited is the genes, which in a suitable environment determine the production of characters. The chromosomes are inherited, the genes are inherited, but the character, whatever it may be, develops under the influence of both genes and environment. In conclusion, therefore, although the underlying principles of Mendelism first enunciated are the essential basis and, as such, are still accepted, we must not think of the genes working out an independent, inevitable, and uncontrollable destiny, but admit a complexity of interacting factors dependent on the environment in which they work.

CHAPTER V

MENDELISM AND MAN

IT has seemed desirable to explain the principles of Mendelism by reference to plants and animals, with which experiments are more easily carried out, and to show how the interpretation of breeding experiments led to Mendelian and chromosome theories. The laws propounded by these theories have been found to apply equally to man. It is extremely unlikely that the principles of Mendelism would ever have been established from the study of human beings, in whom they are neither so easily discovered nor so easily demonstrated, for several reasons. Experiment which involves restriction in the selection of mates is obviously impossible with human beings. Man is a slow breeding animal; there are approximately three generations in a century. In pea plants there is a new generation every year, and in rats, mice, and rabbits probably several a year. The vinegar fly (*Drosophila*), with which a very large number of experiments have been made, may complete its life history in a few weeks. It would take an inordinate amount of time to collect data if we decided to follow up a certain trait in any human family. Whoever began the work would see little more than its beginning. He would also be hampered by shortage of material. Human families are small compared with those of most other animals, and certainly very small in comparison with those of animals normally chosen for experimental purposes. The experimenter would also require surviving records, pedigrees built up from sure knowledge of individuals. How little of this knowledge exists is amazing. Very few people have much knowledge even of grandparents who died some time before them, and still less of great-grandparents. Do we know how tall they were, whether they had blue eyes or brown, straight or curly hair ? The last-named character may, in any event, be a product of art rather than nature. We may hear a good deal of some ancestor's outstanding skill and beauty, but little, or nothing, of unworthy characters. Thus in our only source of material—family history—the required information is frequently absent or misleading. Against inaccurate information must the investigator be always and especially on his guard. If he had reason to think some character was dominant, his investigations would be upset by the erroneous denial of its presence in some individual. A confession of ignorance about the person in question would at least leave the matter open. Any estimate of the nature of the characters, *i.e.* whether dominant, recessive, sex-linked, etc., is based on their behaviour in family histories, *i.e.* on their occurrence, non-occurrence, reappearance, disappearance. Another difficulty is that only characters dependent on single genes can readily be traced through pedigrees.

When a trait does not skip a generation, that is, when any one who inherits it does so from an immediate parent who also shows it, then the trait is most probably dominant. An interesting record exists of an abnormality of the finger joints called symphalangy. This trait has been found to exist in one family for more than five hundred years, and has been handed on as a Mendelian dominant through fourteen generations. This is probably the longest period on record for tracing a Mendelian character in man.

When a trait occurs in some individual (let us call him A) neither of whose parents possessed it, but whose children inherit it, we might consider the possibility of the trait having arisen in A as a mutation. However, knowing how rare is mutation, and that most mutations seem to be recessive, we should not lightly accept such an explanation, but make further inquiry. An examination of the family history might reveal that a brother or sister of A had the same peculiarity. The most likely explanation then would be that the trait depended on recessive genes, which were carried by both of A's parents and brought together (*i.e.* in the homozygous state) in some of their children. The reappearance of such a character in A's children must also be due to the bringing in of the gene from both sides, *i.e.* A's wife must also have carried the recessive gene. Further examination of the pedigree might reveal still other members of the family who possessed the trait in question. Knowledge of the elementary principles of Mendelism should serve to make it clear that a dominant character shows when the genes are in either the homo- or the heterozygous state, but that the recessive shows only in the homozygous state, and that the genes must therefore have been brought in from both sides. The reappearance of characters dependent on recessive genes is more common in cousin marriages than in marriages between unrelated persons. The reason is obvious : similar genes are more likely to be present in near relations because they have the same ancestors from whom to inherit them. This is why cousin marriages *may* be undesirable. If a family bears recessive genes for defects, then the cousin marriage may bring such defects to light by bringing them into a homozygous state. When, however, in plants and animals, close inbreeding brings together recessive genes, the undesirable recessives are thus revealed and discarded while the desirable ones now evident are preserved for breeding purposes; for homozygotes breed true, heterozygotes do not. But the degree of inbreeding that occurs in domesticated animals, with the attendant elimination of undesirables, is inconceivable in man.

If a character is more common in men than in women, and is observed to be handed on from a man, through his daughter, who lacks it, to his grandsons, then it is most probably a recessive sex-linked trait. But one family history alone could not establish a general theory of the nature of inheritance—others must be compared to see if the theory fits them. In fact, not all characters which are commoner in one sex than another are sex-linked.

In human families it is much more difficult to determine whether or not a trait is due to a dominant or recessive gene than in those of other animals. In addition to the already mentioned difficulties associated with restricted opportunity of experiment and smallness of numbers, there is the difficulty that what is apparently the same trait does not behave in the same way in different families. What is diagnosed clinically as the same defect may appear as a dominant in one pedigree and a recessive in another. The cause of this irregularity is not certain, but one of the reasons may be our inability to perceive differences ; different conditions may be erroneously classified as a single condition, and may actually be caused by different genes (either different mutations of the same genes or mutations at a different locus of the chromosome). This difficulty is not unknown among other animals and plants. Very similar effects which may, indeed, appear identical have frequently been traced to changes in separate independent genes. In *Drosophila* two different recessive genes (known actually by the names *forked* and *singed*), which have been located far apart on a chromosome, produce in the homozygous state types of bristle abnormality so similar as to be scarcely distinguishable. Their independence is shown by the fact that an individual heterozygous for both genes lacks the abnormality, although if it be homozygous for either the abnormality appears. Recognition of this phenomenon is important for the understanding of human pedigrees. Moreover, it must be remembered that an abnormal condition may result either from the action of different genes in the usual environment or from the action of unusual environmental influence on an individual of " normal " genetic composition. *Drosophila* again furnishes examples of this phenomenon ; various peculiarities of wings, etc., have been assigned to specific mutations, but similar peculiarities have also been found to occur in the absence of mutations, under certain environmental conditions. A change of environment may perhaps bring about internal changes similar to those caused by a given mutation ; the same processes of development may be affected. In human genetics it is of the utmost importance to remember that a condition (apparently one and the same) which is hereditary in one instance may not be in another ; hence the great importance of a knowledge of family history. Complementary factors, and factors capable of influencing the expression of another factor, are found in man as in other animals. A further difficulty is that all men are very hybrid in nature and do not present the racially pure material that is obtainable in experimental work.

Not all characters which skip a generation are recessive. It may happen that the character in question is one such as Huntingdon's chorea, which does not manifest itself very early in life. Thus a parent who, had he or she lived longer, would have developed it, dies without showing the condition but hands on the gene to children. Moreover, some characters undoubtedly to be considered of a dominant kind do not always show, because of differences in the internal or external environment. A kind of hereditary jaundice behaves as a dominant character, and is often handed on by a parent to half his or her offspring. It may, however, skip a generation. Actually what is handed on as a dominant character is a peculiar kind of fragile blood corpuscles, which render their possessors very likely to develop jaundice if they contract a severe chill or other illness capable of breaking up the red blood corpuscles to such an extent that yellow bile pigment is developed and jaundice ensues.

The difficulties in human genetics are manifold, but in spite of them a good deal of knowledge has been accumulated, so that predictions with a fair degree of certainty can be made in some cases and the chances of reappearance of traits can be estimated.

A few examples may be given. We know that normally two blue-eyed parents can have only blue-eyed children. If one parent is homozygous for brown eyes, then all the children would be brown-eyed, because this parent, being homozygous, must contribute the gene for brown eyes to all children and brown eye colour is dominant over blue. It is, however, difficult to be sure of the homozygosity of a dominant character. In practice we should presume a person to be homozygous for brown eyes if he or she came from a family which had been brown-eyed for generations. Thus, if a brown-eyed Indian married a blue-eyed European it is pretty certain that all their children would be brown-eyed. When both parents are heterozygous with regard to eye colour, their genotypes can be written Bb, where B is the gene for brown eyes, and b for blue. In a mating of Bb with Bb it can readily be seen that the probable percentage of offspring is 50 per cent Bb, 25 per cent BB, 25 per cent bb (*cf.* the peas in Chapter II.). Otherwise expressed, the chance of having brown-eyed children is three times as great as that of having blue-eyed ones. Chance is not certainty, and it *might* happen that these brown-eyed parents would have only blue-eyed children; we should, however, be legitimately surprised. Where disadvantageous abnormalities and defects are concerned, the chance becomes equivalent to risk. If a defect is a recessive character (*e.g.* inherited deaf-mutism), and both parents have it, they must necessarily be homozygous for the defect, and there is no escape for the children. If one parent has the defect and the other is quite free, then the mating could be represented thus: for dd x[1] DD (where d is the gene for the defect and D the dominant allelomorph determining absence of this character), any offspring would have the genotype Dd. If D were completely dominant none of the children would show the defect, but all would be carriers of the recessive gene, which might be handed on for generations. In such a family the mating of near kin might bring the recessive genes together. A cousin marriage might produce children with the defect. A possible pedigree is given :

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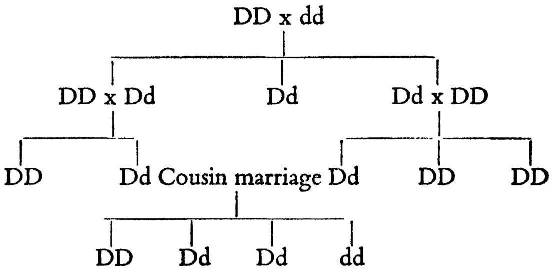
[1] x=Marriage.



The last individual mentioned in this pedigree, the child of a cousin marriage, has the recessive defect. All possible offspring of this cousin marriage have been given in the pedigree in the proportion in which, with very large numbers, they would be likely to occur. However, human families do not provide these very large numbers, and what the last line of the pedigree tells us is that there is a chance of one in four that the child of such a marriage will have the inherited defect. If this defect is deaf-mutism, then a chance of one in four is a serious matter. If D is completely dominant there is no means of telling by inspection the genotypes of the married cousins. As far as observation goes, they might be DD and DD, in which case they could not hand on the gene for deaf-mutism, as they would not possess it. Any means of discrimination between the appearance of heterozygous individuals and those homozygous for the dominant is obviously desirable, so that people from a family where inherited defect of a recessive nature had occurred could know whether or not they were carriers. The position is clearer with a dominant gene, which, if present, betrays its presence. In a family where there is an undesirable dominant trait, an individual free from that trait at least knows that it is not being carried in secret: Once free, always free.[1] For example, in brachydactyly (reduced number of joints on fingers and toes), which is dominant, a pedigree such as that in diagram 13 might be traced. In this pedigree D does not show the trait in question, although his father (C), grandfather (B), and great-grandfather (A) had it. None of D's children can inherit it from him, for he does not possess the gene.

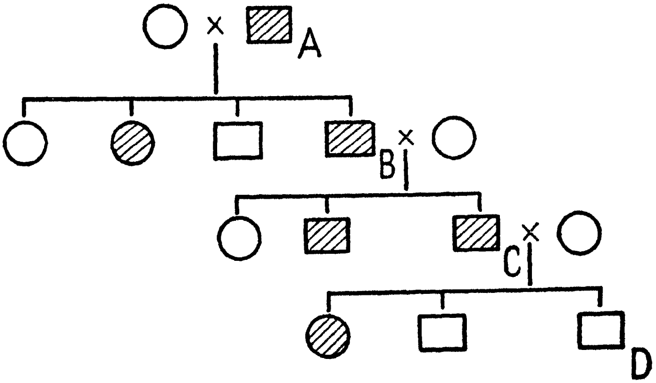


DIAGRAM 13

PEDIGREE SHOWING THE INHERITANCE OF A DOMINANT TRAIT

Circles represent females; squares, males. Individuals shaded possess the trait in question. X = marriage. A, B, C, D serve to identify individuals.

With regard to sex-linked characters also certain predictions can be made. Take colour-blindness, a fairly common character; it has been estimated that about 2½ per cent of the male population are colour-blind. The recessive gene determining it is known to be carried in the x chromosome, of which there are two in women and one in men, the complement to the odd chromosome in man being the smaller y chromosome. If a woman of normal vision, from a family in which there is no colour-blindness, marries a colour-blind man, diagram 14

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[1] It will be remembered that some "dominants" do skip a generation. See page 94.

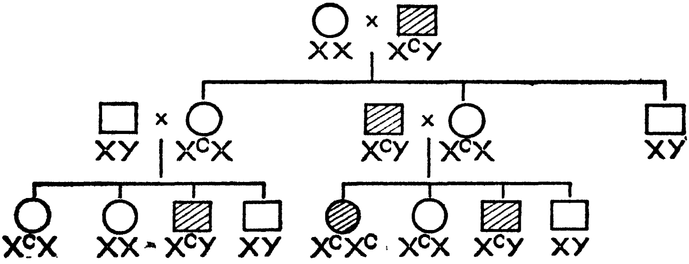

DIAGRAM 14

THE INHERITANCE OF COLOUR-BLINDNESS

Circles represent females, and squares, males. Individuals shaded are colour-blind.

X = X chromosome. Y = Y chromosome. C = gene for colour-blindness. Small x indicates marriage.

shows that neither sons nor daughters would be colour-blind. The sons would not inherit, and would therefore not carry the gene, whereas any daughters, since they inherit the father's x chromosome, would inevitably be carriers. If they married men of normal vision they could have colour-blind sons, and if they married colour-blind men could have both sons and daughters colour-blind. The possible offspring are shown in diagram 14, indicating a possible pedigree. An individual with 2 x chromosomes is a female, one with x and y chromosomes a male. The gene for colour-blindness carried in the x chromosomes is indicated by a small c. The daughter of a colour-blind man is sure to be a carrier, and her sons have a 50 per cent chance of being colour-blind. Other chances can be easily seen by reference to the pedigree. These facts are true for other sex-linked characters such as hæmophilia. For a hæmophilic man to marry and have children, knowing that his daughter would inevitably be a carrier, and that, if she had a son, he would be as likely as not to be hæmophilic, must seem not a little imprudent. A 50 per cent risk, when the penalty is hæmophilia, seems very grave. Obviously in a disease of this kind it is highly desirable to know whether or not a woman is a carrier, because the daughter of a carrier may or may not be so. If normality is incompletely dominant over the recessive defect then a heterozygous woman (carrier) could be distinguished from a woman homozygous for normality. Blood tests have been carried out which suggest that probably all carriers have an increased " coagulation time." A conscientious woman would surely prefer to know the truth. There are other defects of the blood similar to hæmophilia, and therefore a careful diagnosis is necessary. In this defect, as in others, some cases are worse than others, in the same way that some beans are larger than others, even from a closely homozygous stock, because their external environments differ and other factors create different internal environments.

There exists an extensive knowledge of human genetics, and a large number of characters in human beings have been found to depend on single genes. Naturally such work is largely concerned with striking abnormalities, and much of the material is collected through clinics and various institutions.

No attempt is made to give here an exhaustive list of the many characters for which pedigrees have been investigated, and in which Mendelian inheritance has been established and shown to depend on single genes. Among them are a number of anatomical peculiarities, various hair and skin characters, skin diseases, abnormalities of eye and ear, characteristics of the blood system, nerves, and muscles, and peculiarities of body chemistry. Among the anatomical peculiarities are symphalangism (an affection of the joints), lobster claw (split hand and foot), brachydactyly (short fingers, short thumbs, bent little finger), polydactyly (supernumerary fingers and toes), and syndactyly (joined fingers and toes). With regard to abnormalities of the eye, there is no satisfactory simple answer to the question, " Is blindness inherited ? " Blindness may be due to different causes. Some conditions leading to blindness are known to be hereditary and others are not known to be so. Similarly with deafness, there are inherited defects causing deafness, but deafness is not always hereditary ; it may be due to accident or non-inherited disease. A good deal is known about the inheritance of different eye defects which can be clinically diagnosed. Colour-blindness, night-blindness, glaucoma, Leber's disease (optic atrophy), nystagmus (rolling eyeball), and short sight are among the hereditary eye defects.

There are several hereditary defects of the blood system ; of these hæmophilia has already been mentioned. The blood groups are determined by inheritance.

Most people have heard of blood groups because of the publicity given to cases of blood transfusion. Human beings can be classified into four distinct blood groups (O, A, B, AB), the most important differences between them being their behaviour on mixing with other groups. When blood is pumped from one person (x) into another (y) the *erythrocytes* (corpuscles) in the blood of x may be *agglutinated* by the *serum* (liquid) of the blood of y and the consequent interference with the blood flow might be fatal. The blood of another person (z) may, however, mix freely with that of the recipient (y), resulting in successful blood transfusion. It is now known that the blood of members of the group AB may be given to members of this group but not to members of any other ; they are, however, " universal recipients," as their *serum* does not cause agglutination of *erythrocytes* of any of the other groups. Group O are universal donors, but a member of group O cannot receive transfusion from a member of any other group. Group A may give to AB or A, but not to B or O, group B to B or AB, but not to A or O. The biochemical aspect of this knowledge does not concern us here ; its practical value is obvious. The hereditary relationship of the groups is known, and has a legal value in cases of disputed paternity. It is interesting to record that some knowledge of blood groups existed as long ago as the thirteenth century in China, where relationship was tested by a blood mixing method (according to various medico-legal books surviving from that period). Work on blood groups and their distribution in different races is of great interest to students of human evolution, and may throw light on the past history of man. About six years ago J. B. S. Haldane, in a discourse to the Royal

Institution, gave an analysis of the distribution of blood groups in different races and spoke of pre-history in the light of genetics.

Other peculiarities also of body chemistry are hereditarily determined; for example, cystinuria and alcaptonuria (derangements in excretion), and some forms of jaundice. Diseases such as hay fever and other forms of hypersensitiveness (allergic diseases) are inherited, but the condition is often difficult to define and the nature of its inheritance obscure. The hypersensitiveness may be limited to a particular kind of food, eating of which causes the symptoms to appear. If such food were never eaten the existence of the hypersensitiveness might never be revealed. It is said that allergic patients have one advantage in that they possess a general resistance to infectious diseases which is above the normal.

Let us now consider immunity from disease. It is well known that immunity from certain diseases can be acquired for a certain length of time, either by having a mild dose of the disease in question or of a kindred one having a similar effect on the blood, or by inoculation, which confers on the recipient the acquired immunity of another individual. There is also *natural immunity* from (and natural susceptibility to) given diseases in given species. For example, both men and cattle may suffer from tuberculosis, but goats, apparently, are immune, and goat's milk is used by some people for that reason. With any disease due to infection by a bacillus we cannot strictly speak of the inheritance of the disease, but of greater or less susceptibility to infection or of partial or complete immunity. Natural immunity and susceptibility must undoubtedly be of a hereditary nature: some strains of wheat and of other plants are especially chosen for cultivation because of their immunity from disease; some strains of mice develop cancer more readily than others living under similar conditions; different races of men differ in their susceptibility to various diseases. Natural immunity of human beings, however, has not been analysed along Mendelian lines, and we do not know the nature and number of genes involved. Many characters, indeed, defy Mendelian analysis, and other methods of investigation of inheritance must be used. Mendelian methods are suitable for the investigation of characters which show discontinuous variation, *i.e.* when it is possible to affirm that a character is either present or absent. Such a character may not be developed to an identical degree in all people who show it, on account of differences in both the internal and external environment, but where complete dominance is concerned it is possible to place people in two mutually exclusive categories of " haves " and " have nots," and, in the case of incomplete dominance, to place the heterozygotes in a third group. The Mendelian method can also be used for characters depending on more than one gene, provided they be not so numerous as to defy analysis, *e.g.* for those depending on complementary factors. But the Mendelian method will not avail us in the study of the inheritance of characters which show *continuous* variations, *i.e.* in which, within certain limits, all grades of development are to be found. We cannot use the Mendelian method to find out whether stature or size of feet is inherited. Nor can we use it to investigate the inheritance of intelligence, for intelligence appears to be distributed in the population as a continuous variation. The method of studying continuous variations will be considered in the next chapter.

CHAPTER VI

THE INHERITANCE OF CONTINUOUS VARIATIONS: BIOMETRICS

IF we wish to know whether stature is inherited and, if so, to what extent, consideration of individual cases will not help us much. We are sure to find great variety in height among the sons and daughters of tall, short, and medium-sized parents. How can we arrive at any law? It cannot be said of human stature, as of the peas in Mendel's experiments, that tallness is either present or absent. No; apart from abnormalities of dwarfish and gigantic stature, which can be placed in categories apart, we should find continuous gradation from very short men to very tall ones. Investigation along Mendelian lines cannot be carried out. How then shall we attempt to discover whether or not tall fathers have, on the average, tall sons? We must resort to a method which we owe in the first instance to Francis Galton (Charles Darwin's cousin), a method involving numerous measurements and known as the *biometric method* (Greek, *bios*, life; *metron*, measure). Galton was a contemporary of Mendel; they were born in the same year, 1822, but neither can have known much, if anything, of the other's work. Indeed they used very different methods of attacking the problems of inheritance, and it was not until later that the connection between them was realized and understood; for some time the facts obtained by their different methods seemed inconsistent. The biometric method can appropriately be illustrated by reference to human stature, a character early investigated by Galton, who described its distribution and inheritance.

We must begin by considering the distribution of stature in the population, *i.e.* the proportion of men of different heights, the average height, etc. If we wished to know the average height of the men of Great Britain between the ages of twenty-three and fifty we should need a large army of helpers to measure these millions of men. In practice, estimates of average height are obtained from the measurement of random samples. The obtaining of a random sample is not as easy as might, at first, be thought. If we hoped to get a random sample by standing at the corner of the street and asking every seventh man who passed by if, in the interests of science, he would consent to be measured, we might not even so get a representative sample. This would depend on the street and the time of day. In the early morning there might be only manual workers on their way to work; later in the morning perhaps there would be largely city office workers, and there would probably not be any rural workers at all. If there are any differences in average height between different types of workers the sample would not be typical of the nation. It is necessary also to guard against accepting as typical a sample from one place which might contain more of one racial type than of another. Different investigators have found slightly different average heights in the samples they have taken. However, if we obtained a large representative sample of men from different places in the British Isles it might be found that the heights ranged from as much as 77 inches to as little as 57 inches. This was the actual range found on measuring a total of 8,585 British men (English, Irish, Scotch, and Welsh) during the survey organized by the British Association for the Advancement of Science (Report presented 1885).

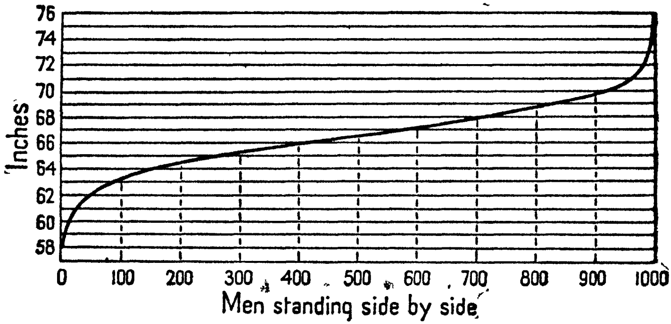

DIAGRAM 15

The horizontal scale represents the numbers of men, whose heights range from 58 to 76 inches, and who are supposed to be standing side by side. The vertical scale gives the heights in inches from 58 to 76 inches, and the curve thus represents the line joining the tops of the men's heads. The horizontal line is on a smaller scale than the vertical : the men would take up more room than the line suggests.

If a large representative sample of men stood side by side in a long line in order of height it would be found that the line joining the tops of their heads would be curved. It would rise, at first steeply, then gradually, remain almost flat for a space, and rise again, at first gradually and then steeply. This is because there are few small and few tall men, but large numbers near the average height (see diagram 15). The larger the sample the more likely are extremes of stature to be found. As the 8,585 included only two men of height 77 in. and two of height 57 in., a sample of 1,000 men might not include any men of these heights. The frequencies per thousand in the British Association Report figures were :

Height in inches	76	75	74	73	72	71	70	69	68	67	66	65	64	63	62	61	60	59	58
Number of men	1	2	3	9	24	46	75	124	143	155	143	115	78	46	20	9	5	1	1

The average height is 67 in. ; this is also the single height most frequently found, which is called the modal value (or mode), *i.e.* there are more men (measured to the nearest inch below) of height 67 in. than of any other single height.[1] The facts can be shown in a diagram of a different kind from diagram 15. They can be expressed in a distribution curve (see diagram 16). Along the base line are successive heights from 58 to 76 in. Along the vertical axis are numbers of men per thousand of each height. The resultant curve, as in diagram 16, is called a curve of normal distribution. A similar curve would be obtained on graphing the distribution of measurements of any natural quality which varies continuously, *e.g.* weight, chest-girth, span of arms, strength, cephalic index (relationship between height and width of head) in man.

For several reasons it is important to know the variability of a group, and desirable to have a simple measure of such variability for comparison with that of other groups. It can readily be seen that the average stature

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[1] The B.A. Report gives average heights of adult males from 23–50 years thus :

Scotland, 68.71 in. Ireland, 67.90 in. England, 67.36 in. Wales, 66.66 in. Average total, 67.66 in.

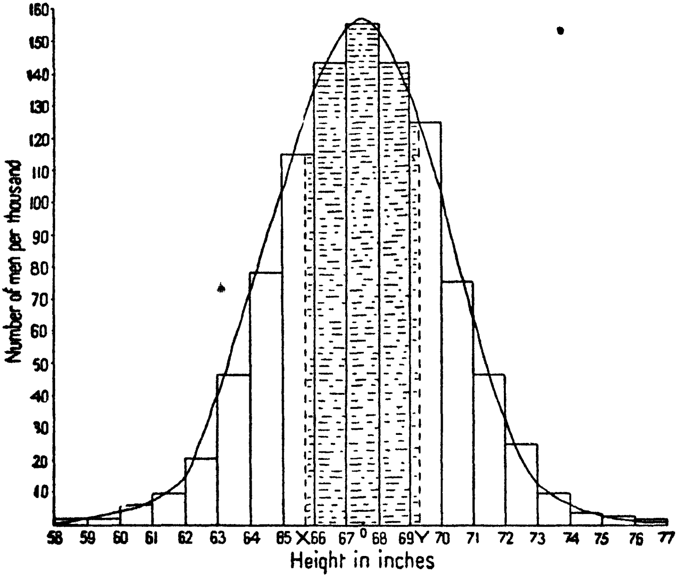

DIAGRAM 16

Curve showing the distribution of stature in men. The rectangles represent the data as provided (*i.e.* the measurement is to the nearest inch), and from them it is easier to see that the shaded area represents half the total area. The area under the curve equals the total area of the rectangles.

and the extremes of variation might be the same with a very different distribution. The variability in British male stature, according to the sample taken, is such that about 44 per cent of the adult male population falls within the range from 66+ in. to 68+ in., and 68 per cent within the range from 65+ in. to 69+ in. One measure of variability is the "probable error," a rather misleading term. It is a probable deviation from the mean, which is as likely to be exceeded as not to be exceeded. In the curve of distribution on page 108 the shaded area represents half the total number of cases. Half the measures fall within it and half without; the distance from O to X or from O to Y is the probable error, X and Y being normally equidistant from O. A measure of variability directly proportional to this, and more frequently used, is the "standard deviation." It is not necessary to enlarge on this subject; it is mentioned merely so that it will be realized that correlation between different groups can only be calculated when the variability is known.

Weight of beans, and numbers of veins in beech leaves, would similarly give a curve of normal distribution when plotted against frequency of such weights or numbers of veins respectively. If we were to shake in a sack 10,000 red marbles and 10,000 green ones, and then take them out at random, ten at a time, it would be found that very rarely, if ever, would ten of one colour come out together, occasionally perhaps nine red and one green, or nine green and one red would come; less rarely, eight of one colour and two of the other, and so on; the most frequent draw being, most probably, five of each colour. These facts could be expressed as a graph by placing combinations of marbles (*i.e.* 10 green; 9 green, 1 red; 8 green, 2 red; etc.) along the base line and frequencies along the vertical. Any such graph would resemble the curve of normal distribution for human stature, and the probable error and standard deviation could in each case be determined. In the drawing of the marbles the assortment may be said to be due to chance, which really means that there are a large number of influencing factors acting independently. Now human stature is dependent on many independent factors, such as the shape and set of numerous bones in various parts of the body which are themselves determined by various influences, including hormones. Some of the influences are environmental, others hereditary.

The extent to which stature can be said to be inherited must now be considered. Suppose a large number of fathers six feet tall were chosen and their sons measured. One son from each, provided he is not specially chosen but taken from the family "at random," would be sufficient. Now the height of these fathers is, according to the average of the sample described above, five inches above the average height. If every son were six feet tall the intensity of inheritance would be complete. Failing this, the heights of the sons must be distributed about some average below six feet, the probable error of the distribution increasing as the average sinks nearer to the average of the whole population. If, however, it were found that the average height of the sons of these tall fathers was 67 in., which is the average of the whole population (according to the sample taken), then one would be justified in saying that stature was not inherited, because the fathers' tallness apparently made no difference to the height of the sons, who were merely of average height. *The actual fact* is that the average height of the sons is *intermediate* between the height of the fathers (6 feet in this instance) and the average of the population (67 in.). What can be said of the sons of short fathers? Are they on the average as short as their fathers, or even shorter? No; on the contrary, they are taller. The average height of the sons of a large group of fathers 5 ft. 3 in. tall would probably be about 5 ft. 5 in., *i.e.* intermediate between the fathers' height and the average height. The sons of short fathers tend to be taller, those of tall fathers shorter, than their fathers. This sounds paradoxical, but is nevertheless true. Such a tendency to regress towards the average is called *filial regression*. It is evident that the more intense the inheritance, the less will be the filial regression, and vice versa. In other words, the amount of regression is an inverse measure of the intensity of inheritance. The facts can be expressed in a graph (see diagram 17). Along the base line are the heights of each group of fathers, and along the vertical the average heights of sons of each group of fathers.[1] If for each group of fathers it were found that the average height of their sons was 5 ft. 7 in., the facts would be represented by the line A B. If the height of sons of each group of fathers was the same as the fathers' height, *i.e.* fathers 5 ft. 2 in., sons 5 ft. 2 in., fathers 6 ft., sons 6 ft., then the line C D would represent the facts; for if this ultimate case were ever reached every son would be the same height as his father. The actual facts, as opposed to these suppositions, are represented by the crosses on the diagram, which, occurring in the angles A O C and B O D, show that the average height of sons of each group of fathers is intermediate between the fathers' height and the average height of the male population. The nearest fitting straight line for these points is the line E F which can be taken to represent the facts. If there were more regression the line E F would lie nearer to

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[1] Direct comparison between the fathers and sons is possible because the standard deviation of each generation is the same.

A B, if less regression E F would lie nearer to C D. The amount of regression is, then, indicated by the slope of the line E F. The angle C O A is 45°, and thus $\frac{\text{C A}}{\text{A O}} = 1$.

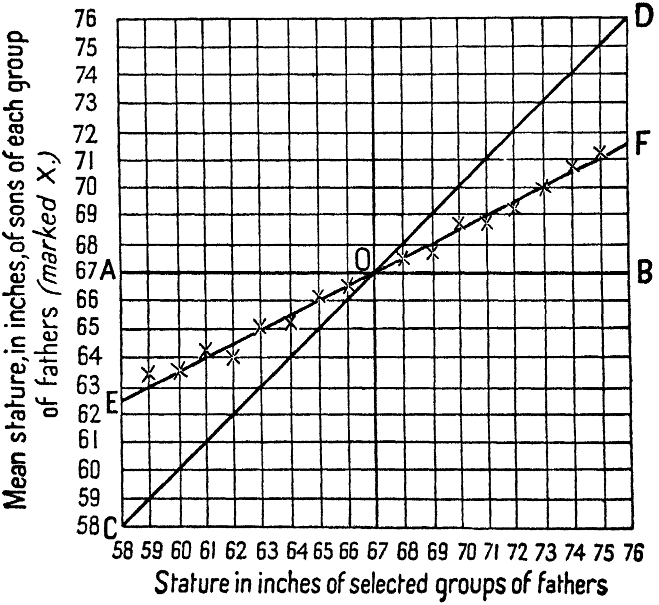


DIAGRAM 17

REGRESSION DIAGRAM SHOWING THE CORRELATION BETWEEN FATHERS AND SONS FOR STATURE

The angle E O A is 22.5°, and thus $\frac{\text{E A}}{\text{OA}} = .5$. This relationship is called the tangent of the angle, and is a convenient way of expressing the slope of the line which makes an angle with the horizontal A O. It gives us the value called the coefficient of correlation, a term which is frequently found in any description of statistical work. The coefficient of correlation for height between fathers and sons is the relationship between the deviation of the sons and the deviation of the fathers from the average of the male population. A parental (paternal) coefficient of correlation of .5 for stature of fathers and sons means that for a group of fathers of any given height the average height of the adult sons is intermediate between this given height and the average height of the male population. If, when correlation coefficients are mentioned, there is conjured up the image of the slope, and it is realized that a small angle with E F approaching A B gives a small correlation coefficient, and a large angle—approaching the maximum of 45°—gives a greater coefficient of correlation, the term may convey more meaning. There can also be negative correlation coefficients where quantities vary in inverse relation to each other. The correlation coefficient can vary between plus 1 and minus 1. In practice mathematical formulæ are used to obtain coefficients of correlation. Biometrics take one into the realm of the complicated mathematics of statistics : attempts to give simple explanations lead to inaccuracy. All that is attempted here is to give some slight indication of the nature of the statistical (or biometric) method of study and a simple explanation of the term "coefficient of correlation." Correlation is a "tendency towards concomitant variation," and the correlation coefficient is a measure, though not always an adequate one, of this tendency.

Although the correlation coefficient may indicate the extent to which two quantities vary in relation to each other, and suggests either the effect of one variable on the other or some common effect on both, greater refinement of method is necessary to analyse the situation further. The relationship between stature of fathers and stature of sons is expressed by a correlation coefficient of .5, but this figure alone gives no indication of the extent to which the relationship is due to similarity of environment or to innate causes. Valuations of the environment and the control of the environment in other species where the relationship of one generation to another is the same suggest that the similarity is due to heredity. In the next chapter it will be seen that a great difficulty in the study of the inheritance of mental characters is that of determining the relative contributions of heredity and environment to the degree of similarity found between parents and children and between siblings (an old English word meaning children of the same parents).

It is perhaps desirable to emphasize a few points over which there might be misunderstanding. Not all the sons of tall fathers are shorter, nor all the sons of short fathers taller than their fathers ; in all cases there is a range from short to tall. Apart from a remote probability we can say nothing for the individual. The laws of regression tell us only about masses, not about individuals. On the average the tall father is more likely to have tall sons, the short father short sons, but it is not certain, and we can predict nothing certain in the individual case. Nothing has yet been said of the stature of mothers or of daughters. Women on the whole are not as tall as men, but when adjustment is made (by reckoning what a woman's stature would have been had she been a man), the correlation coefficients for stature for mother and son or daughter, and for father and son or daughter all work out at approximately .5. Sometimes an imaginary " mid-parent " is used, which is the mean of the father's and mother's stature (adjusted value), and the correlation coefficient calculated, which is, as we should expect, higher than in the case of a single parent. Similarly fraternal correlation coefficients are found which give a measure of the similarity between siblings. For a variety of characters fraternal correlation coefficients of .5 have been obtained.

The facts related in this chapter and those of Mendelism are not inconsistent, and the bridge which links them and makes it possible to interpret all facts of inheritance in terms of chromosomes and genes is the theory of multiple factors (see pages 77ff). The instance of the inheritance of ear length in corn, studied by East, may be quoted. Two fairly pure types of maize were crossed, one with short cob (5–8 cms.), the other with long cob (13–31 cms.) ; the variation within each group can be considered as largely due to environment, since the strains are relatively pure and homozygous. In the F_1 generation the cobs were intermediate in length, ranging actually from 9 to 15 cms. The variability is no greater than that of either parent, while the mean is about half-way between their means. Inbreeding in the F_1 generation gave an F_2 with approximately the same mean as F_1 but with much increased variability. In fact the range covered practically the whole range of both parents of F_1. This example is typical of many cases of the inheritance of size factors which have been investigated. It shows the blending inheritance so commonly found, and the differences in variability. The intermediate nature of F_1, and the rise in variability in F_2, where the parental types again appear, are both significant facts, and give a clue to the nature of the inheritance. The reappearance of parental types in F_2 suggests segregation of genetic factors already explained in connection with early breeding experiments, where parental types, due to recessive factors, reappeared in the second generation after a cross. This type of size-inheritance can be explained by assuming that there are a number of factors acting cumulatively to produce size, and segregating independently; such factors are called multiple factors.

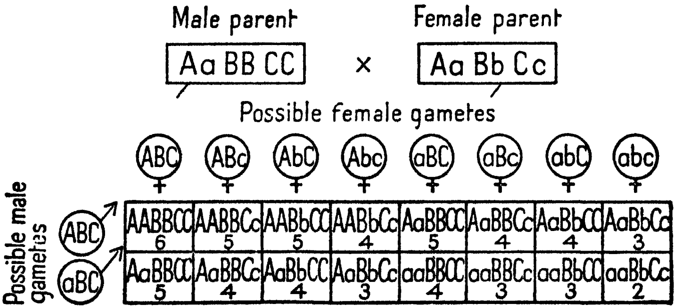
A further example showing colour-inheritance may be given. This example was mentioned on page 77. A cross between wheat plants with white and those with deep red grains gives in F_1 those of intermediate colour, and in F_2 there is, if large numbers are involved, full range of colour and reappearance of parental types. Diagram 12, page 79, illustrates the position where two factor pairs are involved, but in some cases three factor pairs operate. Representing these factor pairs as AA, BB, and CC, and the allelomorphs as aa, bb, and cc, a dark red parent would be AABBCC and a white one aabbcc. On crossing these the F_1 generation, intermediate in colour, would be AaBbCc. On inbreeding, the F_2 generation would, if large numbers were involved, be expected to have the full range from white to full red colour. Compare with diagram 5, where three independently assorting pairs of factors are involved, reading A, B, C, a, b, c, for T, G, S, t, g, s, respectively.

Similarly, on crossing negro with "white," the offspring—mulattos—are intermediate in colour; in subsequent generations there is more variability, and it is theoretically possible to get white or black offspring again from mulatto parents. The number of factor pairs involved is, however, not known.

Now, to show the consistency between the Mendelian and biometric methods of studying heredity, imagine that each of the factors A, B and C in the wheat adds an equal amount, say one degree, to the intensity of colour. The homozygous dominant (AABBCC) having six degrees of colour intensity is red, whereas the homozygous recessive (aabbcc) having no such degrees is white. Suppose the average of a mixed population has three degrees of colour intensity. If an individual of factorial composition AABBCc (*i.e.* with five degrees of colour and thus two above the mean) is crossed with one AaBbCc (*i.e.* with three degrees and thus average), diagram 18 would represent the possible offspring and, given large numbers, the mathematically probable proportions. The range of colour is from two degrees to six (full red colour), and in subsequent generations white grains might reappear. The average is $\frac{64}{16} = 4$ degrees of intensity, which is one degree above the mean, and intermediate between the one parent having five degrees—which is two above the mean—and the average of the population (three degrees), which was also the colour of one parent. With two identical homozygous parents, say AAbbcc and AAbbcc, the offspring and parents would be identical and the question of regression would not arise. With two average (heterozygous) parents, AaBbCc and AaBbCc it is possible to have offspring of full colour, but the chances are only one in sixty-four compared with one in sixteen in the progeny shown in diagram 18.

Here we have a simple parallel to filial regression in human stature, but it is not an analogy that can be pressed too far and must not be allowed to give a false impression that the problem itself is simple. The analogy is given merely to indicate that blending and segregation are both to be explained by a comprehensive chromosome or genetic theory of inheritance.

The distribution and inheritance of human stature are far more complicated than the colour-inheritance in wheat grains just described. It is not known how many factor pairs are involved, nor the extent to which these are dominant or recessive in nature. Evidence suggests that the factors for tallness are largely recessive : the least variable offspring are the children of two tall parents, whereas tall mated with short, or short with short, give more variable offspring owing to the recessive factors for tallness carried by the short parent. Colour-inheritance



	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
ABC	AABBCC 6	AABBCc 5	AABbCC 5	AABbCc 4	AaBBCC 5	AaBBCc 4	AaBbCC 4	AaBbCc 3
aBC	AaBBCC 5	AaBBCc 4	AaBbCC 4	AaBbCc 3	aaBBCC 4	aaBBCc 3	aaBbCC 3	aaBbCc 2

DIAGRAM 18

The checker-board represents the possible offspring from a cross between two wheat plants of genetic composition **AaBBCC** and **AaBbCc** with regard to colour of grain. The figures represent degrees of colour. See text.

in wheat grains was a simple and straightforward case of known genetic composition. Moreover, the effect of environment was not considered, nor was the possibility of the tendency for like to marry like (assortive mating). A slight positive correlation for stature between mothers and fathers has been found in several samples measured. All this makes regression and correlation more complicated than, perhaps, the simple outline description of this chapter would suggest. When there are many independently assorting factor pairs, such as must be involved in the determination of human stature and other continuous variations, the number of different possible segregations and recombinations is very large, and the chance of any offspring completely resembling a parent or ancestor diminishes in proportion to the number of factors involved. The inheritance of height, or of any other continuous variation, may be compared to the " hands " dealt from a pack of cards. Imagine the pack of fifty-two cards depleted of the aces, kings, and queens, leaving forty cards which are dealt to four players, giving ten each. Imagine another pack depleted of the 2's, 3's and 4's, and similarly dealt. The second set of players would have a much better chance of a " good hand " than would the first set. Chance, however, might actually result in some member of the first set having a better hand than some member of the second set. Statistics inform us about masses and averages, but they tell us nothing certain of the individual. With regard to stature we can but say that tall parents are more likely than short parents to have tall children, short parents more likely than tall to have short children, but chance might give a result similar to the hands of cards described. Segregation can play strange tricks.

Galton explained regression by our mixed ancestry. Each one of us has two parents, four grandparents, and—unless intermarriage has taken place—eight great-grandparents, sixteen great-great-grandparents, and 1,024 tenth great-grandparents. Going back in this way we should have to admit a population of thousands of billions a few thousand years ago, and we know that such a population did not exist. We have far fewer ancestors than are theoretically possible, because our ancestors intermarried. Anyone who is the child of a cousin marriage has six, not eight, great-grandparents. Even allowing for intermarriage, however, each of us is the product of mixed ancestry. Galton expressed it thus: "In every population that intermarries freely, when the genealogy of any man is traced far backwards, his ancestry will be found to consist of such varied elements that they are indistinguishable from a sample taken at haphazard from the general population." Pearson expressed the same facts in saying, "A man is not only the product of his father, but of all his past ancestry, and unless very careful selection has taken place the mean of that ancestry is probably not far from that of the general population. In the tenth generation a man has (theoretically) 1,024 tenth great-grandparents. He is eventually the product of a population of this size, and their mean can hardly differ from that of the general population. It is the heavy weight of this mediocre ancestry which causes the son of an exceptional father to regress towards the general population mean; it is the balance of this sturdy commonplaceness which enables the son of a degenerate father to escape the whole burden of the parental ill." These explanations must not be allowed to suggest the idea of dilution or concentration as in the mixing of liquids. All Mendelian work emphasizes the existence of indivisible units—the genes. Our long line of mixed ancestry gives each of us the chance of containing a greater assortment of different genes. Mendelian studies have shown us that these segregate at random in reduction division, and mate at random in fertilization. No mating can create genes which are not already there in either parent ; it can but bring together existing ones. In some " strains " there are more genes for tallness, in others more for shortness. Persons of the former type are more likely to have tall children, those of the latter to have short. There is no such thing as a pure race of human beings ; we are all of a hybrid nature, but the purer a race tends to be for any particular character the less likely are we to find dissimilarity between parents and children. *If* we could find a family where both a man and his wife and all their known ancestors were tall, we should be legitimately surprised if they had short children.

The facts of regression show the statistical resemblance that exists between one generation and another unless special characteristics are selected for survival. They also indicate the importance of selection. If tall men marry tall women, and of their sons the tall again marry tall women, and so on for generations, then a race of tall people could be established, and regression for this character would be virtually eliminated. They would not go on getting taller and taller *ad infinitum* and thus develop a race of giants. They would tend to become more homozygous for tall genes, thus more homogeneous in respect of this character of height, but the effects of selection would be limited by the genes on which selection acted. It would not be any good setting out to breed a race of tall people if the race from which we started had no genes for tallness. However, who would want to breed such a race, and who would control the breeding ?

Johannsen's work on " pure lines " is of interest in this connection. He found, on examination, that the beans growing in a garden patch represented a mixed population from which various " pure lines " could be extracted. Taking the beans as a whole and weighing their seeds he found a normal distribution of weights. When heavy beans were selected the average weight of beans among the offspring was higher than the average of the whole, and yet showed the same regression to mediocrity observed in the case of human stature. Similarly, the average weight of the offspring of light beans was less than the average of the whole, but also showed regression. By selecting tall or short beans for many generations a more or less homogeneous stock of either could be obtained; in fact, several pure lines could be established, and the average seed weight of each differed from the general average. Within a pure line it does not matter whether we grow from a heavy or a light bean; the average of the offspring is the same, because the stock is, more or less, homozygous. When the members of homologous pairs of chromosomes go to opposite poles, there separate identical, not opposite, members of allelomorphic pairs of genes determining weight, and fertilization can only bring together similar members. Not all the beans within a pure line are equal in weight: there is a normal distribution of weight. These differences are, however, due to differences in environment, *e.g.* time of fertilization, amount of food received, position in the pod, etc.; these differences are not inherited, as we have just seen that the heavy or light bean within a pure line gives offspring of the same average value. The position can be summarized by saying that the differences within a pure line are due to environment, and the differences (in averages) between pure lines are genetic, *i.e.* due to differences in inheritance.

We are thus, in the light of these experiments, in a better position to understand the causes which give rise to the normal distribution of height in a mixed population like that of our own country, and why this distribution resembles any distribution due to " chance." There are causes at work similar to those operating on the beans ; some are environmental, some are genetic. In the original population of beans it could not be told by mere inspection whether the differences were genetic or not ; this could be discovered only by means of careful experiment, by the results of breeding, by measuring the amount of regression.

We have seen that there is reason to believe that the differences in stature in our population are partly genetic, and thus the average stature of the nation can be affected by selection, conscious or otherwise, for survival, as parents of the next generation, of tall or short men.

It has been estimated that the average stature of Frenchmen was lower by two inches at the beginning of this century than it was a hundred years before. This estimate may or may not be correct, but it seems pretty certain that biologically France was considerably impoverished by the wars of the Republic and the First Empire. We do not yet know the extent of the biological effects of the Great War, but it is obvious that modern warfare is biologically disastrous. It does not cut off the weak individuals at the expense of the strong, as hand-to-hand fighting might do, but it exposes those of better physique to greater risks of death, and thereby increases the death-rate of the strong. The weaker are left behind in more sheltered positions, and the character of the next generation depends largely on the men who are left.

A good deal has been said of stature to illustrate a method of study and to indicate some implications of the facts revealed. The laws hold good for any other physical characters which have been measured. Our next problem is the inheritance of mental characters, and this will be considered in the following chapter.

We have seen that, when differences between individuals are genetic, selection can effect changes in a population. It is therefore important to know which differences in a population are genetic. Another important subject for investigation is that of the processes of selection which may be at work in any community. In non-civilized and primitive communities the physical—and to some extent mental—characters are kept up to a high level by natural selection and the elimination of the unfit. Selection in a civilized community is very different and may be dysgenic instead of eugenic. Some aspects of this problem will be considered later.

CHAPTER VII

THE INHERITANCE OF MENTAL CHARACTERS

WORK along Mendelian lines has furnished examples of mental abnormalities dependent upon single gene changes. Such instances are, however, not common. A rare malady known as juvenile amaurotic idiocy, resulting in blindness, idiocy, and early death, has been found to depend on a single recessive gene, appearing only in the homozygous condition. It has been traced in several families where there were cousin marriages bringing together the two recessive genes whose presence was unsuspected. Goddard, an American worker, has suggested that one form of mental defect is due to homozygosity of a single recessive gene. This contention is disputed, but, considering the frequency of mental defect among the offspring of mental defectives, the genes determining hereditary mental defect appear to be, on the whole, recessive. Undoubtedly numerous genes are involved, and mental defect has as yet scarcely been analysed from a genetic standpoint. Clinically, not all cases of mental defect can be placed in one category; they are of different degrees and kinds, and due to different causes. Diagnosis may be difficult. Accidents and diseases, particularly in childhood, may lead to mental defect, which is not heritable unless the disease which causes it is so. But in a considerable proportion of cases mental defect appears to be hereditary; and, as with other hereditarily determined conditions, the proportion of defect is greater among the children of consanguineous parents. Owing to the difficulties of diagnosis and the differences of definition of mental defect the extent to which it is hereditary is not exactly known. As there are different degrees of the condition, individuals are classified into various grades. In the Mental Deficiency Act of 1927 classification (with accompanying definitions) was into the grades: (1) idiots, (2) imbeciles, (3) feeble-minded, and a separate group (4) moral defectives. This classification has no biological significance, and each group includes defectives of many different kinds. In the first three categories the classification is largely based on mental age; for mental deficiency can be considered as arrested development. The subject of mental age will be discussed presently (page 135). However, the criterion for mental defect is not solely lack of intelligence judged by tests; other aspects of the mind have to be considered. The legal definition of mental defect in children has an educational implication—it concerns their educability; whereas in adults it has a social implication, and concerns their need of supervision for the protection of themselves and others. It was estimated in the Government Committee Report of 1929 that among mental defectives about 5 per cent are idiots, about 20 per cent imbeciles, and the remaining 75 per cent comprise the varying grades of feeble-mindedness.

The proportions depend on the somewhat arbitrary deliminations of the groups, and so does the estimate of the proportion of mental defectives to normal people. The Mental Deficiency Committee of 1929 estimated the incidence of all kinds of mental deficiency at 6.7 per thousand of the population in urban areas and 10.5 per thousand in rural areas, and estimated 2.9 per thousand incapable of earning an independent livelihood. For school children the proportions given were 20.9 per thousand in towns and 39.7 per thousand in rural areas. The difference is due to the different definitions of feeble-mindedness: educationally a child may be considered defective because he has an I.Q. below 70 (see page 135), whereas when adult he or she may not be certified defective on social grounds. The proportion of mental defect appears to have increased in recent years. The increase is undoubtedly more apparent than real, because methods of determination have changed. Admitting this, however, it is generally agreed that there is some real increase, which is doubtless due largely to the greater fertility of some feeble-minded people compared with the fertility of those of greater intelligence. (See also Chapter VIII.). Classification is not always easy. Where higher grade mental defectives are concerned, there is often doubt whether or not the term " defective " should be applied. It is often difficult to decide whether or not a child should be sent to a special school instead of to an ordinary elementary school. Grading shows that every degree of deviation from the normal is found, and the differences may be of degree rather than of kind. However, Tredgold suggests that it may be more correct to regard the differences as differences of kind, and to think of mental deficiency at one end of the scale and genius at the other as lying outside the normal range. The Government Report on mental deficiency (1929) draws attention to the fact that whereas the proportion of higher grade mental defectives (feeble-minded) seems to be greater among groups of people of low mentality in " lower " social grades (" the social problem group "), the lower grade defectives (idiots and imbeciles) are found indiscriminately in all social grades. Perhaps, then, the lower grade defectives should form a group apart, whereas the higher grade ones form part of a continuous variation merging imperceptibly into the dull and sub-average as do these into average people.

Insanity—also variable in its causes—is a very different condition from feeble-mindedness ; it is not a general arrest of development. However, according to Gates, an unusually high percentage of feeble-minded become insane. Insanity occurs in highly sensitive minds, in which the balance producing stability is easily upset. Feeble-mindedness is at the opposite end of the scale to genius, but insanity and genius may not be widely separated. There is much psychological and medical literature dealing with the inheritance of various kinds of insanity.

Many people will admit the inheritance of physical characters in man, and even of mental *abnormalities*. They are, however, less ready to admit in *general* the inheritance of mental characters, attributing the ordinary run of mental differences to differences of environment and opportunity. There is great inconsistency in the views of many people where mental characters are concerned. There is a tendency to accept what favours their own case and to reject what would discredit themselves or their opinions. Although the subject has aroused interest from early times, it was not until last century that scientific inquiry of any value was made, when Francis Galton made an extensive systematic inquiry into the inheritance of mental ability. This was published in 1869 under the title of *Hereditary Genius*. A more suitable title, which he admitted in the 1892 edition of his work, would have been, "The Inheritance of Great Ability." Galton had already drawn attention to the inequality of man, saying that he had "no patience with the hypothesis occasionally expressed and often implied, especially in tales written to teach children to be good, that babies are born pretty much alike, and that the sole agencies in creating differences between boy and boy and man and man are steady application and moral effort."

The arguments by which Galton endeavoured to prove that great ability was hereditary consisted in showing "how large is the number of instances in which men who are more or less illustrious have eminent kinsfolk." Scientific works quickly become out of date, and Galton's work has been, in a sense, superseded by work using greater refinement of measurement; but it still forms most interesting reading, and is of historical importance. It directed attention to the subject of human heredity. He accepted, giving his reasons, high reputation as a fair test of high ability. He estimated the proportion of men who could be called eminent by comparing the numbers of men whom the world honoured, as indicated by the *Dictionary of Men of the Time*, with the whole male population between suitable ages. He also consulted the obituary of the year 1868, published in the *Times* on January 1, 1869, comparing the number of men's names therein with the number of men who died annually in Great Britain. He took as the lower age-limit forty-five, to facilitate comparisons. In each case the proportions worked out more or less the same, viz. about 250 to 1,000,000, or 1 in 4,000. "Eminence," then, is a quantitative measure; it means that a man stands out as at least

1 in 4,000. If the achievement of eminence were due purely to chance, like winning a lottery prize, it would be exceedingly rare for two members of a family to achieve it. For more than two of a family to do so, and that on many occasions, would certainly suggest that something other than chance was responsible. Achievement of success does, in fact, appear to run in families. It seems, therefore, not to be a result of pure chance, but to be determined by some underlying cause which makes one family more likely than another to achieve it. This cause may be either advantages of environment or inherited ability. Galton contended that in the case of the *most* eminent people social advantages, however effective, could not alone have maintained them in the positions they had reached. For these and other reasons Galton maintained that, at least in the cases of very high ability, not environment but inherited capacity was responsible for there being several eminent members of a family. He traced a gradual rise in ability where marriages were consentient to its production, and a gradual falling off through successive generations. He considered these facts to be more representative than the admitted sudden appearance of eminence in an undistinguished family. Galton drew up a chart of distribution of ability in the population, giving a curve of normal distribution. We may note that a similar curve is obtained in all public examinations where there are many candidates. Perhaps Galton did not sufficiently estimate the influence of environment, family traditions, and nepotism, but after the publication of his work no one could with justice deny completely the inheritance of mental ability. Some people still do so, however, and assert, in spite of all evidence to the contrary, that we are all born equal, and

become different solely because of our different surroundings.

Other work has been done along similar lines. Some was begun with intent to confute Galton, but confirmed the general conclusion that mental ability is inherited. Of course one can point to numerous men and women who have risen from undistinguished stock to positions of eminence. But mediocrity is plentiful, and the *proportion* of eminent children to eminent parents is greater than the proportion of eminent children to mediocre parents. As for real genius, it is exceedingly rare, and must depend on some extraordinary combination of genes. We know that it has frequently arisen from undistinguished stock. Galton believed it was more common in families of high ability, and gave illustrations.

On the whole, the chief interest of Galton today is historical—he was an originator. His aristocratic bias led him to methods of investigation that are open to criticism. If he had lived today, when the social ladder is wider and family influence has less effect on the individual's success, he might have investigated along different lines, and avoided certain untenable arguments and conclusions. His general contention, however, that mental ability is inherited, would not have been affected, though he would have been less confident about his identification of ability and distinction.

One of Galton's pupils, Karl Pearson, was an early worker in the field. At the beginning of this century he published in the journal, *Biometrika*, the results of an extensive inquiry about ordinary everyday people—school children, nearly four thousand of them, in various schools throughout Great Britain. He employed statistical methods similar to those used by Galton for human stature. He realized the difficulty of obtaining data for parental correlation coefficients, the only source of information being the grandparents, who, even if available, might not be unbiased. He resorted therefore to fraternal correlation coefficients (see page 115). He obtained his material by sending out a large number of questionnaires to schools whose staffs were willing to co-operate, asking for information about brothers and sisters, concerning physical characters (such as height, weight, eye colour, cephalic index) and mental characters (such as performance in different school subjects, general intelligence and temperament). Inquiry about handwriting was also made. The estimates of intelligence and of such qualities as vivacity and assertiveness could not be made according to any objective quantitative scale, and were admittedly based upon the opinions of the teachers. However, some check was exercised by asking more than one teacher to estimate (independently) the same pupils, and a surprising degree of unanimity was obtained. The results showed that an intelligent child is more likely to have an intelligent than a dull brother or sister, and vice versa for the dull child. But it must never be forgotten that nothing can be predicted for the individual. By the use of such scales of measurement of intelligence and other qualities the facts were expressed in terms of correlation coefficients. For all characters, *both physical and mental*, approximately the same coefficient of .5 was obtained. As has already been explained (Chapter VI.), the correlation coefficient merely gives a measure of the relationship between two variables (say, two sets of measurements), but does not explain the cause of the relationship. However, as the degree of similarity of siblings is closely the same for all characters—such as eye colour, which cannot normally be influenced by environment—as well as for mental characters, which are subject to such influences, Pearson considered these facts to suggest strongly that inheritance is in all cases more responsible than environment for the resemblances found.

Many independent investigations have been carried out. An early one by Schuster and Elderton—pupils of Karl Pearson—compared the performance of fathers and sons in the Oxford Honour B.A. degree examinations. The Oxford Historical Register between 1830 and 1892 was consulted, and the degrees of all men whose fathers also had been at Oxford were compared with the fathers' degrees. The results showed remarkable correspondence between the performance of fathers and sons.

Other workers have compared the examination performance and scholarship records of siblings, obtaining similar results. Estimation of ability by examination results may not seem very satisfactory, as the validity of examination results and their value as tests of real ability are often questioned. However, in an examination with standardized marking, one can at least claim that a type of mental ability is measured.

A difficulty in all work on the inheritance of mental characters is the definition and measurement of the characteristics compared. It is not as simple a matter to measure a man's mind as to measure his body. Mental characters depend on one another in intimate ways, and depend for their development, as do all characters, upon the environment. The mental equipment cannot be measured independently of the environment. We can measure capacity to respond only by measuring response. The latter depends not only on innate capacity but on experience acquired from the environment.

A few years after Pearson's work an American psychologist, Thorndike, measured the resemblance of siblings, using various "mental tests." Some were designed to show the influence of training and school work (*e.g.* tests in multiplication and addition), while others were tests of abilities considered to be relatively independent of training (*e.g.* memory tests). The degree of similarity of siblings was closely the same in each case. This suggests that the similarity was due primarily to similarity of parentage (*i.e.* heredity) rather than to similarity of environment. The use of "mental tests" was a step forward on the lines of more objective measurement.

Intelligence Tests and Their Use

The work on mental inheritance has gained enormously in precision by the use of standardized "performance tests" and "intelligence tests" to compare the abilities of siblings, and of parents and children.

Individual intelligence tests and the method of standardizing them were first devised by Binet and Simon, two Frenchmen interested in the work and education of sub-normal children. In 1904 they set to work to devise diagnostic tests and to grade intelligence. Great strides were made in America during the Great War, when group tests of intelligence were devised and applied to soldiers and recruits. In "group tests" large numbers are tested simultaneously by written tests. Altogether in America nearly 1¾ million men were tested during the war. The idea behind the work was that men incapable of further training could be sorted out, and some indication be given of the type and extent of training which would be worth while. The tests proved useful, and great confidence was established in the predictive value of intelligence tests. A number of other tests have since been devised by various workers with a view to finding the ability or capacity, as originally proposed by Binet and Simon, " to judge well, to understand properly, to reason well." They considered these the essential springs of intelligence, but they included other qualities such as initiative and " practical sense," or adaptability to novel situations. All this agrees with common-sense ideas on intelligence. By means of intelligence tests a " mental age " and intelligence quotient can be assigned to an individual. These matters cannot be understood without considerable explanation, but, briefly, one may say that the mental age is determined by performance in standardized intelligence tests. The standard is based on the average score of marks obtained by a typical group of a given age. The mental age divided by the chronological age gives the mental ratio, and this multiplied by 100 (*i.e.* expressed as a percentage) gives the *intelligence quotient* (popularly known as the I.Q.). For adults, in fact for all over sixteen years of age, the chronological age (*i.e.* the denominator of the fraction) is usually taken as sixteen, because of the belief that maturity of intelligence is practically complete at about the age of sixteen years. There is some disagreement about the actual chronological age at which intelligence reaches its full maturity; but intelligence probably matures at about sixteen years of age on the average. In the super-normal mind the age of maturity of intelligence is later. Those with such minds may reach a mental age of sixteen at the chronological age of twelve, and go on developing to a mental age of eighteen or more. Mental growth does not proceed uniformly, but slackens down as we approach sixteen. The I.Q. remains relatively constant in spite of schooling. Apparently the function of education is not to raise intelligence, but rather to see that intelligence is properly used. Though for normal children the I.Q. varies but little over a period of several years, for gifted children it appears to become slightly greater and for sub-normal ones to decline. The subject of mental growth and maturity is of supreme importance in the matter of choosing candidates for higher education. It is generally recognized that some flower early, some late.

This digression on intelligence tests is necessary to an understanding of their use in work on inheritance. A mental age of seven in a child of seven corresponds to an I.Q. of 100, but a mental age of seven in a child of ten corresponds to an I.Q. of 70, and is on the border line of "mental deficiency." It is amazing to think that a number of adults with a mental age of seven or eight are parents. School children below 70 in I.Q. are generally considered mentally defective. Burt has concluded from evidence provided by a revised Binet scale and other tests that an I.Q. above 115 or 120 indicates at least Central School ability, whereas one of 130 or 135 represents the standard for Secondary School scholarships. An I.Q. above 150 is rare, and Burt, who is a most extensive worker, recorded some years ago that he had discovered only one I.Q. of 190. Cattell, having tested thousands of children and adults over several years, has only twice encountered an I.Q. of 200. As the different tests have not been satisfactorily standardized, we cannot justly compare the different figures or take any of them as absolute values.

There is considerable difference of opinion on the nature of intelligence and the meaning of the word. Intelligence tests are used as measures by people holding divergent views on the nature of intelligence. We are familiar with the phenomenon of measurement without understanding of the fundamental nature of the thing measured. Measurements of electricity have long been in use, but there is still lack of unanimity on the subject of its nature. Some psychologists regard intelligence as a single ability common to all intellectual processes, others as a group of several abilities, of which some are more general than others. Others regard it as having no real identity, but as being a convenient term to express the average of many specific abilities. One thing seems to be agreed, that success in intelligence tests is a sign of high intelligence. They have been found to have good prognostic value, for example, in the case of the American army tests. Duff worked on the "follow up" of children who showed high intelligence in the Northumberland tests (see pages 158ff). The later careers of those who made high scores in intelligence tests, compared with those who made average scores, were on the whole what one could expect from more intelligent people. The tests have not in all individual cases, however, good prognostic value, and have been criticized accordingly. Their prognostic value is diminished because of subtle traits of character which affect performance, so that those who do not make a good performance in them may yet be successful in life. On the contrary, some children who show high intelligence in the tests fail to make good because they lack moral and other qualities necessary for success. Moreover, the disciplinary conditions under which the tests are taken have a marked effect on performance. Although the tests suffer from weaknesses, they are the best measures of intelligence which psychologists have devised ; they give a quantitative measure which is more objective than previous judgments. They can be used to gain a knowledge of the inheritance of intelligence and of the distribution of intelligence in a population.[1]

The use of intelligence tests to determine fraternal or parental correlation coefficients is a step forward in the task of measuring and comparing innate qualities as distinct from acquirements from the environment. Intelligence can, however, only be measured in an environment which gives it scope. The tests do attempt to minimize the importance of the environment, and give the greatest possible credit for that indefinable innate quality called intelligence which gives to its possessor the power to act with judgment, understanding, and reason. A great difficulty in designing tests is the difference in environment of those tested. Many intelligent English people would be unable to answer some simple American tests because of unfamiliarity with the vocabulary. Similarly between different social classes the barrier of vocabulary and experience of common things can be so great that the designing of tests is rendered difficult. The tests are questions—simple tasks concerning everyday things selected from the background of experience which is assumed to be common to all the children tested. Obviously there is great difficulty in choosing a common background of experience for gipsy children, canal barge children, average elementary school pupils, and those attending preparatory schools. In spite of the difficulties involved in devising tests to measure general

[1] Aspects of the latter question will be discussed in the next chapter.

intelligence by response to questions and problems on everyday topics, a good number exist which are reliable in that they yield the same results with the same people on different occasions, and satisfactory in that they agree with other ratings of intelligence. These are important criteria of the satisfactory nature of a test. Some intelligence tests are developed along pictorial rather than linguistic lines, others require the performance of some task with concrete material, and are described as "performance tests." This practically eliminates the vocabulary difficulty and minimizes any advantage enjoyed by the children of the cultured home when responding to verbal tests.

Much work on resemblance of siblings has been done with these standardized intelligence tests, their advantage over other tests being that not only actual marks can be compared, but also mental age and I.Q. In general fraternal correlation coefficients for I.Q. of .5 or thereabouts are obtained. With tests suitable for adults the I.Q. of parents and children can be compared ; this was done about ten years ago by Jones in California and in 1938 by Cattell in England.

We have seen that the measurement of mental qualities and the estimation of similarities between groups of individuals is difficult, but that the difficulties have been considerably diminished by the use of standardized intelligence tests. The primary difficulty, however, in all work on mental inheritance is to discover how far similarities are due to environment and how far to inheritance. It is a commonplace to say that the individual is a product of the interplay of heredity and environment. His reactions to environment are determined, not only by his initial equipment, but by his subsequent experiences. Theoretically there are two general methods of studying the problem. The first would be to keep the environment constant from birth for people of very different ancestry, and measure the amount of similarity or difference between them at the end of a given period. The second would be to vary the environment—with control of conditions—of people of the same ancestry, and note the consequent similarities and differences. Such conditions are not attainable. We cannot thus isolate a group, nor, if that were possible, could we say that the environment of each individual was identical. We do sometimes find a group of children whose environment in an institution has been more uniform than that of most; investigation of institution children will be described presently. In general the best that can be done is to measure the resemblances and differences of people of one ancestry compared with those of another living under approximately the same conditions. Such, more or less, have been the terms accepted in most of the investigations described, and all indicate that mental ability, general intelligence, is inherited to the same extent as stature, the relationship being expressed by a fraternal correlation coefficient of approximately .5. The evidence would be stronger and equivalent to proof if one could show that with closer degree of relationship the resemblance became stronger. Galton gives evidence of this kind in *Hereditary Genius*, showing that there were on the average more eminent relations in close degree of relationship to an eminent man than in more remote degree. Those whose claim to distinction hangs on one eminent ancestor generations ago depend on a flimsy thread.

Twins

Much more convincing evidence comes from a study of twins, one type of which represents the closest possible human relationship. Galton recognized the value of twin studies, and distinguished between the two kinds of twins ; since his time many other workers have used twins for their investigations.

Galton obtained his information on twins by the questionnaire method, depending on records and anecdotes that people were willing to give. Thorndike's work in 1905 represented an advance in so far as he used direct measurement by means of " mental tests," such as adding, subtracting, and various word tests. He found a greater degree of resemblance betwen twins than between ordinary siblings. He showed that older twins were no more alike than younger ones, that twins did not resemble each other more in abilities dependent on training than in those which were relatively independent of training. He concluded that greater similarity of upbringing was not responsible for the greater resemblance between twins than between ordinary siblings—the explanation lay in their greater similarity of genetic composition.

The use of standardized intelligence tests on twins represents a further step forward, and nineteen years after Thorndike's work there was an investigation of much interest and importance by Merriman, who worked out the correlation coefficients in I.Q., as judged by score in intelligence tests, for twins of the same sex as well as for all twin pairs ; he found a much greater degree of similarity for like-sex than for unlike-sex pairs. His work threw light on a problem about which there is now general agreement. Biologically twins are of two different kinds, viz. ordinary fraternal twins (dizygotic), and so-called identical twins (monozygotic or uni-ovular). The first kind are formed by independent fertilization of two separate ova by two spermatozoa, and are not therefore more likely to be similar in genetic composition than are two ordinary siblings. Such twins may be of the same or of different sex. The monozygotic twins are due to the splitting, at a very early stage of development, of a single fertilized egg. It can readily be seen that identical twins will have the same chromosome make-up, *i.e.* they are *genetically identical.* Any differences between them can legitimately be ascribed to the environment, ante- or post-natal.[1] Our knowledge of the chromosome determination of sex makes it obvious that identical twins are always of the same sex.

Merriman's work has been commented on and followed up by other workers. Taking identical (*i.e.* physically indistinguishable) twins as a separate group, a remarkable degree of resemblance is found in mental characters. Correlation coefficients in I.Q. as high as .9 have been obtained. In fact the resemblance is almost as great as that between performances of the same individual on different occasions. But non-identical twins, whether of the same or of opposite sex, show approximately only the same degree of resemblance as ordinary siblings. Some workers have found a slightly higher degree of resemblance, attributable, no doubt, to the greater similarity of their environment ; they are treated more alike at home and have the same " age-position " in the family.

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[1] Recent work indicates that the ante-natal environment is responsible for many differences between uni-ovular twins.

Identical twins brought up apart since infancy furnish material of unique value in this nature-nurture problem, but surprisingly few cases are found. Newman and Muller have given records of such twins from time to time in the *Journal of Heredity*. These cases and others have recently (1937) been written up in *Twins: A Study of Heredity and Environment*, by Newman, Freeman, and Holzinger. It is a valuable contribution to the literature on twins by a psychologist, a statistician, and a specialist in the biology of twins. It concerns the history of nineteen pairs of separated identical twins. Although the average difference in I.Q. between such identical twins is little greater than for those brought up together, which might suggest that the influence of environment is slight, generalizations of value cannot be made from such small numbers. Moreover, it is extremely important to realize that some pairs show wide differences in I.Q.

The general impression given by work on twin resemblances, however, is that, as far as scores in intelligence tests are concerned, heredity far more than environment is responsible for the degree of resemblance found. The close similarity in intelligence of identical twins is the most convincing evidence that mental characters are inherited in the same manner as physical ones, and that, although their development is in all cases dependent on the environment, they are primarily dependent on genes.

The Effect of Similarity of Environment

Other researches which throw light on the question of the effect of environment on intelligence are those on foster-children and children in institutions. Some investigators have found no change in I.Q., others a slight and scarcely significant one, when children were removed from bad homes to institutions, or adopted from inferior homes into better ones. The children's educational achievement, however, usually improves considerably with improved environment. Some investigators have found a significant correlation between the I.Q. of foster-parents and foster-children, but the extent to which this is due to attempts to place children with foster-parents of similar intelligence to their real parents is not known. Obviously this is a field for study.

In any attempt to measure the relative influence of heredity and environment, estimation of the environment is extremely difficult. We have no measures of environmental influences throughout the lives of the people tested, and cannot know how far they are essentially similar though separate. Environments superficially similar may be essentially different—individuals tend to create their own environment. However, when children of very different ancestry are brought up together in what appears to be a closely similar environment, there is good material for investigation. Tests of various kinds have been given to children in orphanages and other institutions, where they may have been almost since birth in a fairly uniform environment. The variability in I.Q. for these institution children has been found approximately the same as that for samples of children brought up in their own homes. The environment of the institution may be closely similar for all but it does not produce greater uniformity in intelligence.

It is of interest to mention in this connection observations on the effects of equal training on people of different capacity. Experimental work has shown that, for example, with simple arithmetic and word tests the greatest improvement after a period of equal practice has been made by those with the highest initial score. Statistical studies of the scholastic records of pupils show the extent to which they maintain their relative positions. Records throughout a year have been made on pupils of different school classes. The pupils of one class were divided into groups according to their initial performances and received, throughout a year, the same teaching in arithmetic. Periodic tests of ability showed gradually increasing differences between the groups, and at the end of the year there were big differences in their achievement. The gain from teaching is proportionate to the ability to learn. Equal practice does not smooth out differences in ability or tend to make pupils more equal; rather does it emphasize the differences between them. Two children may enter an elementary school alike in their ignorance of school subjects; one may end up as a casual labourer and the other as a brilliant engineer. Experienced workers with mental defectives find that there is a point beyond which development in these people seems impossible. Yet hardly anyone need entertain anxiety about the possible extent of his abilities, as so few of us have ever developed our abilities to their full extent along the right lines.

We must, then, recognize a normal distribution of intelligence, and no equalizing of environments would make everyone equal. Differences of intelligence cannot be smoothed out in this way. If all the candidates in an examination got nearly equal marks, this would suggest that, in teaching, good pupils had been retarded that the poorer ones might " catch up." If nearly all got full marks, the examination, unless a merely qualifying one, would be a bad one, because it did not give scope to superior intelligence to show its superiority.

If even a restricted environment allows individual differences to show, a rich and full environment accentuates them. Slow and dull individuals fail to use opportunities, whereas bright and intelligent ones do so, and progress in proportion to their intelligence. Gladys Schwezinger has pithily expressed it thus : " If a low grade moron were put into a college classroom he would probably get nothing out of the professor's lecture ; if placed in a moving-picture house, he might respond with interest to the horse-play on the picture. If a superior adult were placed before such a picture he might go to sleep, but in the lecture-room he would add to his store of knowledge. A meagre environment might not affect him in a positive way, but a richer environment would affect him in a stimulating way. To the moron an intellectually stimulating environment is no asset and a meagre environment is no handicap."

Moral and Other Traits

It is sometimes said that moral qualities are inherited. Our minds are concerned in the making of decisions of a moral nature. The cases of the Jukes, the Nams, the Hickories, and other degenerate families are cited as examples. Dugdale has thus described the Jukes: " From one lazy vagabond named Juke born in 1720, whose two sons married into a family of five degenerate sisters, six generations, numbering about 1,200 persons of every grade of idleness, viciousness, lewdness, pauperism, disease, idiocy, insanity, and criminality were traced. Of the total seven generations 300 died in infancy; 310 were professional paupers, kept in almshouses a total of 2,300 years; 440 were physically wrecked by their own 'diseased wickedness'; more than half the women fell into prostitution; 130 were convicted criminals; 60 were thieves; 7 were murderers; only 20 learned a trade, 10 of these in a state prison, and all at a state cost of over 1,250,000 dollars."

We cannot attribute all this dismal record to the genes of one lazy vagabond born in 1720. Successive generations had lived in a bad environment and married into degenerate families.

In dealing with moral qualities, while here again we find the now familiar interaction of heredity and environment, it seems that the influence for good or bad of environment is stronger than in the case of intelligence. Inherited characters might determine largely the behaviour in particular circumstances. Instincts vary in strength from individual to individual. Social behaviour depends to a considerable degree on the " sublimation " of instincts, *i.e.* the canalization of the instinctive response into socially useful channels. The resultant action will be partly dependent on the strength of the original instinct. Some natures cannot easily withstand temptation; some do not distinguish " right " from " wrong." Burt, however, in his study of delinquent children found delinquency more often associated with defective discipline in the home than with any other single cause. Faulty handling in early childhood leads to maladjustment which unenlightened home discipline cannot overcome, hence the necessity of child guidance clinics. Burt's discovery that delinquent children had a greater proportion of delinquent parents than had non-delinquent children may be explained by imitation of parents by children as well as by heredity. The defective home discipline so commonly associated with juvenile crime may itself be a product of the parents' bad inheritance. The problem is very intricate and involved. Burt has said, " Some natures remain unsoiled though sunk for years in mud : others are porous and penetrable ; and the grime works into the grain. It is the personal reaction to the given situation that makes a man a criminal, not the situation itself. It is not bad surroundings that create delinquency, but the workings of these bad surroundings on the thoughts and feelings of a susceptible mind . . . inner personal weaknesses which give to these outer environmental factors their power to work their worst." That the " susceptible mind " and the " inner personal weaknesses " are largely dependent on hereditary factors gains impressive support from the evidence of Lange's work on criminal twins, translated into English by Charlotte Haldane under the title of *Crime as Destiny*.

In Bavarian prisons all prisoners who were twins were reported, and other sources were searched for records of twin pairs of which one at least had been in prison. Thirty pairs—thirteen monozygotic (*i.e.* identical) and seventeen dizygotic—were discovered on whom adequate information was available, and of each pair one at least, *i.e.* the subject first investigated, had been imprisoned.

Among the thirteen monozygotic pairs the second twin also had been imprisoned in ten cases, whereas among the seventeen dizygotic pairs the second twin had been imprisoned in only two cases. " This," says Lange, " leads us to the following conclusion : in as far as crime is concerned monozygotic twins on the whole react in a definitely similar manner, dizygotic twins behave quite differently. If, therefore, we attach importance to the twin method of investigation, we must admit that as far as the causes of crime are concerned, innate tendencies play a preponderant part." In addition to providing evidence on the nature-nurture problem the facts help us to realize the necessity for a changed attitude towards crime. Admittedly it has changed considerably during recent years : psychologists and psychiatrists in child guidance clinics deal with problems of juvenile delinquency.

A man may find it almost as difficult to keep out of the hands of the law as to add a cubit to his stature. The criminal twins were constitutionally alike in their inability to organize their lives in ordinary surroundings so as to keep out of the hands of the law. A specially sheltered environment would be necessary to keep such people from crime. For the majority of us, however, the attitude to destiny need not be one of resignation in the face of an overwhelming torrent. Recognition of differences might lead to a determination to make the most of one's gifts and to avoid temptations to which one seemed especially prone to succumb. Most of us have weaknesses and compensations. Similarly, in the intellectual sphere it is no good sitting back and refusing to try because one knows that one could never paint like Leonardo da Vinci or play the violin like Kreisler.

Returning for a moment to institution children, although it appears that institutional life has no appreciable effect on intelligence, there are other considerations of extreme importance. Several workers have justly contended that institution life as opposed to family life may produce considerable differences in emotional and temperamental traits that go to make up personality, such as initiative, resourcefulness, and self-reliance—traits that, like intelligence, tend to be hereditary.

We have seen that there is no agreement on the fundamental nature of intelligence, but that intelligence tests are widely admitted to be a good basis of measurement of it. Neither is there any generally accepted definition of personality—psychologists do not agree on an analysis of it. Moreover, so far, there is little agreement about the possibility of its measurement. Psychologists are at work in devising tests by which it is hoped to measure personality and develop some scale for comparison of individuals. The tests so far suggested are of various kinds, and include questionnaires on interests and on attitudes to various social questions, also observation of overt reactions during tests and interviews. Methods of psychoanalysis have also been employed. Some tests are of a physiological nature, and instruments are used to record inner physiological changes associated with emotional activity. Development of such tests has followed Cannon's work describing bodily changes in animals in states of pain, hunger, fear, and rage.

Character and personality are influenced partly by temperament. Temperament, in its turn, depends partly on the hormones secreted by the endocrine glands (see Chapter IV.). The extent of development, and consequently the amount of secretion of these glands, has been shown to depend on genes. As the amount of secretion affects not only the appearance but the temperament and emotional disposition of the individual, these characters are thus brought into the orbit of hereditary influences. Persistent over-secretion of thyroid leads to great energy and excitability, but liability to exhibit signs of strain. Insufficiency of thyroid leads to dullness and laziness. We have seen that emotions such as fear and rage are associated with increase in the amount of adrenalin in the blood.

Standardized tests for personality traits are unquestionably inferior to intelligence tests. In fact they are not yet sufficiently developed to be of much practical use except for diagnostic purposes in clinical work, and perhaps for schoolroom use. It seems unlikely that we shall ever have a simple quantitative scale of measurement of personality, for it depends upon the subtle interaction of so many factors. The tests are developing and improving, and in time they may be of use in problems of inheritance and in larger problems of the quality of population. Their use in these respects is, of course, rendered more difficult by the influence of environment. All psychological work indicates the greater influence of environment in the development of personality and character than in the development of intelligence. We have no satisfactory scale of measurement of this environment.

Conclusions

There is, then, ample evidence that the foundations of intelligence, personality, and character are determined by heredity, although the direction which their development takes depends in varying degrees on circumstances. No environment could make an Abraham Lincoln out of a typical Juke any more than it could make a great musician out of a man who was born tone deaf. Nor could Einstein's genius, had he been born into a primitive community, have developed along the lines it has followed.

It is of absorbing interest to try to determine relative influences of heredity and environment. The facts of this chapter, particularly those concerning identical twins, indicate that, in general, intelligence as measured by intelligence tests is little affected by training, but individual cases show us that it is not completely independent of the environment. Considering that it is measured by tests which include acquirement from the environment, this latter fact is not surprising. Rather is it surprising that intelligence thus measured seems to be so little affected by the environment ; even some extreme differences appear to alter the I.Q. very little.[1]

Lange's work suggests that, where some traits of character are concerned, ordinary differences of environment may have little effect. Either member of a pair of his criminal identical twins would have needed to have a very different environment from that of the other to escape crime. However, a different environment and treatment of the twins (compatible with their enjoying any liberty) which would have kept them from crime might prove beyond man's ingenuity to devise. Care is necessary, however, in arguing from extreme cases to more nearly average ones. Facts recorded in this chapter indicate that the intelligent profit more than the dull from richness of environment. Similarly, in personality traits, alteration of environment would most probably have more effect on those with more potentiality.

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[1] Severe illnesses such as epilepsy (which may not be of a hereditary nature) and sleepy sickness (*encephalitis lethargica*) may have a considerable effect on intelligence.

It may be repeated that caution is necessary in making general statements about the relative influence of heredity and environment. Fundamentally this is an individual problem to discover within a stated environment how much variation differences in heredity will cause, and conversely, with a given heredity, how much variation changes in environment can produce. It is of the utmost importance to realize the statistical nature of the facts brought forward in this chapter. We could all no doubt cite individual cases which are not in accordance with general findings. One might assert, " I have repeatedly found it so . . .," but this is no measure unless we know the number of times it is not so.

A character depending on the cumulative effect of many genes cannot be predicted, as the possibilities are so numerous. They are even more numerous with the subtle interactions of effect which occur in mental characters. The analogy of the pack of cards is relevant for mental as for physical characters, even though we might have to postulate an extraordinary game where cards differ from their face value according to their association. Just as the tall man may have sons of any height, so the intelligent parents may have children of any I.Q., but are more likely to have intelligent ones than dull. We are apparently born with a potentiality to develop a certain level of intelligence, just as we are born to be tall or short according to our genes, and unless environmental conditions determine otherwise we develop this height and this I.Q.

Each has a right to the place his intelligence and character can secure for him. Unfortunately the constitution of society is such that the " poor hand " from the " good pack " frequently gets privileges and favours that are denied to the " good hand " from the " poor pack." With a knowledge of the mode of inheritance of physical and mental characters and of their dependence, in many cases, on numerous genes segregating independently, it is easy to see how ill-founded is the " Nordic myth." There is little likelihood that the mental and physical characters supposed to be the prerogative of the " Nordic race " may still, after considerable crossing and independent segregation, be mutually associated, even if they ever were. For them to remain associated would demand their dependence on the same genes.

Finally, with regard to the inheritance of mental ability and the various traits of personality and character, we have to remember that, whatever we are or become, we have developed from a single cell—the union of two gametes—and these cells are the only physical link between one generation and the next. Mental activity appears to be fundamentally a problem of biology, largely of biochemistry. Even if the mind is not a mere by-product of matter and is something which, in an unknown way, transcends it, yet the facts at least suggest, and forcibly so, that the material basis of mind is subject to the same laws of inheritance as the body.

Although the names of some authors and investigators are cited in this and other chapters, no attempt is made to give an exhaustive account of work on the subject of mental heredity. The work is too vast, the workers too numerous, for a complete survey in one chapter of a volume of this size and scope. Some indication is given of the gradual progress and the present position of this study. Many results concern small numbers, and considered alone would have no generalization value. It is of importance, however, to realize that practically all the evidence is in the same direction.

CHAPTER VIII

INTELLIGENCE AND SOCIAL CLASS

GALTON'S work on human heredity led him to take a serious view of our national inheritance and the possibility of its decline. He coined the word "eugenics," defining it as the study of agencies under social control which may improve or impair, either physically or mentally, the racial qualities of future generations.

There has been much unfounded talk about hereditarily superior and inferior stocks and the innate qualities of the various social grades and groups. Fortunately there has also been serious investigation. Cyril Burt investigated the problem in 1909. Binet and Simon commented on it in 1911. They compared the results obtained by themselves on testing Parisian children with those obtained by Decroly and Degaud when giving the same tests to Belgian children. The results obtained by the Belgian children were markedly superior, and the cause and nature of this superiority were sought. It was suggested that perhaps the tests had been marked not in accordance with the scale but too liberally. However, the reason undoubtedly appeared to be superior intelligence. The Parisian children were from an elementary school, the Belgian ones from a small private school attended largely by children of professors, doctors, lawyers, and other people of "superior" social standing.

It is difficult to classify into social groups the children tested. Some investigators, for example, Cyril Burt, have compared children attending different types of schools. Other workers have tried to classify the children on the basis of the parents' income or of the father's occupation.

The 1909 investigation by Burt compared the performance, in tests designed to measure "general intelligence," of children in a "good class" elementary school and of those in a preparatory school. Burt found that the performance of the preparatory school boys was on the average superior. Later he compared performances in tests of children in two elementary schools in the same London borough. One was a slum school and the other drew its pupils mostly from families ranking among the "best" which send their children to an elementary school. The children from the latter school scored higher in all tests except one, which involved a "trap" to catch the unwary. Burt, commenting on this, said "the slum child unblushingly recognizes that the examiner is setting a trap for him. The child of nicer manners hardly entertains such a suspicion and conscientiously searches for minute differences." This interpretation of the difference in scores admits the effect of training. It has already been pointed out how difficult it is to measure intelligence alone. Since the days when the first tests were given, however, a considerable amount of work has been done on the designing of tests.

Pressey and Ralston published in 1919 the results of testing more than 500 children whose parental occupations were classified into four groups: (1) professional, (2) executive, (3) artisan, (4) labouring. The results showed, on the *average*, superiority of children of professional parents over those of labouring parents in answering the tests given; the children of the executive and artisan groups were intermediate between these.

A large-scale investigation of this nature was carried out by Duff and Thomson, and the record of it was published in the *British Journal of Psychology* in 1923 under the title of "Social and Geographical Distribution of Intelligence in Northumberland." A brief description of this work may be given.

On a given day a test was taken by all children between the ages of eleven and thirteen years attending elementary schools in Northumberland (excluding Newcastle and Tynemouth), and by most pupils between those ages in secondary schools: 13,220 elementary and 405 secondary school pupils were tested. Of these, thirty papers were spoiled—it was presumably found that the conditions required had not been kept—leaving a total of 13,595.

The test was designed as an intelligence test and the results expressed in terms of the pupils' I.Q. Realizing the difficulties of defining and measuring intelligence, the authors of this work point out that "intelligence" must only be taken to mean the particular qualities measured by a particular intelligence test.

As the numbers were so large the individual I.Q.'s were not published, but they were grouped into eight classes, the numbers in each group being as follows:[1]

				No. of children.
Class A +	=	I.Q.	140 or over	16
„ A	=	„	130 to 139	129
„ B +	=	„	120 „ 129	732
„ B	=	„	110 „ 119	2,275
„ C +	=	„	100 „ 109	3,598
„ C −	=	„	90 „ 99	3,536
„ D	=	„	80 „ 89	1,972
„ D −	=	„	below 80	1,337

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[1] Observe the approach to normal distribution described in Chapter VI.

Teachers were asked to state the occupations of each child's parent ; in 176 cases this was not given or was obscure. The remaining 13,419 children were grouped according to the parents' occupation and the average I.Q. for each group obtained. The average I.Q. for all the 13,419 children was 99.6. The occupations were grouped at first into about ninety different classes. Then the occupations of similar standing were placed together. This grouping was done to show as far as possible differences of social standing, of skill, and of responsibility, but it will readily be understood that the information available was not always sufficient for accuracy. This regrouping produced thirteen different classes. The numbers of children with parents in these classes are given on the following page, together with the distribution of I.Q.'s and the average I.Q. for each group. Some occupations difficult to classify are omitted.

It will be seen that there is a steady change in *average* I.Q. with difference in social standing in so far as this is indicated by the groupings. It cannot, however, be too strongly emphasized that *nothing can be predicted of the individual.* It is important to realize that every occupational grade contains children of high and low intelligence.

An attempt was made to classify the children into two groups according to their parents' occupations ; " brain-work " and " hand-work " were the two rough occupational divisions made. The first included those whose occupation was " writing, teaching, giving orders, or selling," and the second group those whose occupation was " making, mending, moving, growing, or tending any kind of goods." The results were as follows :

Brain-work .	**1,722 children,**	**average**	**I.Q.**	**=**	**106.6**
Hand-work .	**10,848 „**	**„**	**„**	**=**	**98.6**

	I.Q. < 100		I.Q. = 100		I.Q. > 100				Total.	Average I.Q.
	D−	D	C−	C+	B	B+	A	A+		
A Professional	4	6	10	34	42	33	7	1	137	112.2
B Managers	3	5	13	20	32	12	6	1	92	110.0
C Higher commercial class	13	16	56	96	108	62	14	3	368	109.3
D Army, navy, police, postmen	3	10	30	42	28	11	5	0	129	105.5
E Shopkeeping class . .	27	74	164	202	187	77	14	3	748	105.0
F Engineers	45	58	117	173	119	49	7	3	571	102.9
G Foremen	10	31	56	87	60	7	5	0	256	102.7
H Building trades . . .	49	75	196	195	140	52	9	1	717	102.0
I Metal workers, shipbuilders	61	94	223	235	160	40	7	0	820	100.9
J Miscellaneous industrial workers	40	57	122	145	76	26	5	1	472	100.6
K Miners and quarrymen, excluding managers, foremen, etc. . . .	684	1,028	1,662	1,494	866	206	25	3	5,968	97.6
L Agriculture, all classes .	143	193	313	264	149	53	13	0	1,128	97.6
M Low grade occupations, labourers	171	239	336	291	128	44	5	0	1,214	96.0

The distribution of I.Q.'s was as follows :[1]

I.Q. = 100

	D−	D	C−	C+	B	B+	A	A+	Total No of Children
Brain .	61	140	321	478	459	204	51	8	1,722
Hand .	1,160	1,700	2,964	2,815	1,655	475	71	8	10,848

Again let it be noticed that although the *average* I.Q. is a little higher for children of "brain-workers" the distribution shows that each group contains children of all grades of intelligence. This enormous overlap is frequently missed, ignored, or misrepresented in discussion of the differences in intelligence between different social grades. There is no justification for a permanent social hierarchy which assumes the innate and universal superiority of any social class. There is no ground for assuming that a given member of any class must be, by virtue of his social origin, inferior or superior in intelligence and ability to a member of any other class. The overlap is itself evidence of the genetic nature of intelligence. If intelligence were determined by environment, a higher correlation of intelligence and social class would be expected. Whatever be the clear-cut distinctions between social classes they are not distinctions of intelligence.

As for geographical distribution, high intelligence is commoner in urban areas, and in the most rural areas, than on the coal-field. There is some evidence that the superiority—in percentage of more intelligent children—of the residential suburbs is due to selection from surrounding districts. People climbing the social ladder move in to the suburbs, and this selection has affected the coal-field more than the remoter rural areas. This draining of rural areas as the intelligent are attracted to the towns seems to be a lamentably universal tendency. We have seen in Chapter VII. that the incidence of mental deficiency is higher in rural than in urban areas.

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[1] For significance of classes A, B, etc., see table on page 158.

This investigation serves to show some of the difficulties which beset those investigating such questions. Recognition of the difficulties may alter the frame of mind in which criticism is made.

About the same time as the above report came out two American workers, Haggerty and Nash, published a record of their investigation into " Mental Capacity of Children and Paternal Occupation." Their study included testing of 8,021 school children, and their results were similar to those of Duff and Thomson.

Gray and Moshinsky found similar mean differences, with the same extensive overlap, between the intelligence of different social groups. They show, however, the " considerable inequalities between the educational opportunities open to able children of the more prosperous social classes and those available to equally able children for whose higher education the financial assistance of the State is required." Further discussion of this aspect will be deferred to the final chapter. Gray and Moshinsky adopted the following classification of parents' occupations, and found a progressively descending average in I.Q. : (1) Professional, (2) Larger business owners and the higher executives of business, (3) Clerical and commercial employees, (4) Minor professional and other highly skilled workers, (5) Shopkeepers, (6) Skilled manual workers, (7) Smaller business owners, (8) Unskilled manual workers. They draw attention to the necessity for caution in interpreting averages, for " In a great many cases single occupational groups show a much higher and much lower mean I.Q. than the average of the socio-economic category in which they have been put." In their London inquiry it was shown that the children of advertising workers, insurance agents, seamen, engineering draughtsmen, and the clerical grades of the Civil Service exceeded the average of the class ranked highest in average intelligence, namely, professional workers. On the other hand, certain professional occupations, *e.g.* ministers of religion, were much below the average of their group. As the numbers in some of the groups were very small, the conclusions must necessarily be of doubtful reliability. Intelligence and " socio-economic status " are certainly not correlated at every point on the social scale. " Measured by a purely pecuniary canon, or in terms of the influence they exert in public life, the class of wealthy business men stands highest in the social hierarchy. Nevertheless, their children are nowhere reported to have a higher I.Q. than those of professional workers, even of school teachers, whose income and social status are comparatively low."

Other investigations have been carried out, and the results agree in showing that on the average children of " lower " social status do less well in intelligence tests than those of " higher " status. Here arises the problem of the effect of environment—particularly out-of-school environment—on performance in tests. Several investigations have been made on children of different parentage in a standard environment. In the previous chapter it was recorded that orphanage children showed the same degree of variability in intelligence as a normal sample of children brought up in the more varied environment of their own homes. The average resemblance in intelligence between siblings in orphanages and those in their own homes has been found to be the same. Now the standard environment offered by orphanages and other institutions has been used to estimate the environmental influences in this question of the correlation between intelligence and social class. Jones and Carr-Saunders found, among orphanage children who had not lived with their parents for years, a positive correlation between greater intelligence in children and " higher " social class of parent. This strongly suggests that the correlation usually found is due to innate factors rather than to home environment. It would appear, however, that the environment is not without effect. This investigation actually indicated a slight positive correlation between length of residence and increase in I.Q. among children of poorer homes, but a slight negative correlation between length of residence and I.Q. for children of "better" social classes. This environmental effect is, however, *slight*, nor is there reason to suppose that the environmental effect is of major importance in determining the different averages of intelligence, as indicated by intelligence tests, of children from different social classes.

Another interesting investigation along similar lines was carried out by Evelyn Lawrence. She selected for inquiry institutions of different kinds, all of which took children very young—almost from birth. She divided the fathers into five occupational groups, similar to the grouping in the Registrar-General's reports, as follows: (A) is the professional class; (B) includes tradesmen, clerks, and highly skilled artisans; (C) is a large middle group of skilled and semi-skilled workers;

(D) comprises unskilled workers ; and (E) is a residual group including dock labourers, street pedlars, gypsies, and paupers. Some may think the groups so wide as to be in effect a useless classification, and there is bound to be doubt about the group in which to place some occupations. The distribution of intelligence quotients showed discrepancies of various kinds, but in general it emerged that " though a child has never lived with its parents it is likely, other things being equal, to have a *slightly*[1] higher intelligence if it comes from one of the so-called upper classes than if it is the child of labouring people." The degree of association between parents and children is, however, slightly smaller for institution children than for non-institution ones, which suggests that environment has some slight effect. The main cause of the correlation between intelligence and social class appears to be biological rather than cultural, innate rather than environmental. This investigation shows, as all similar ones have shown, the *enormous overlap* between the classes. It is merely the average intelligence which differs : each class stretches through all grades of intelligence. How dangerous would be any inference about individuals is shown by the fact that, in Miss Lawrence's study, when the fourteen children with I.Q. above 135 and the twenty-eight children with I.Q. below 70 were considered, it was found that the parents of the former in no case belonged to the " A " group, only two (or three) to the " B " group, and the rest came from grades " C " and " D." The parents of the dull and deficient children were, however, also from groups " C " and " D."

It is known from census returns and other sources that the birth-rate of the " lower " classes is greater than that of the " upper " classes. The facts of the previous chapter show that mental ability, as judged by performance in intelligence tests, is inherited, and the facts of this chapter show that it is less common in those social groups of greater fertility. This means that there must be a tendency for the average intelligence of the population to decline.

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[1] The italics are mine.

The extensive Merseyside survey carried out under the direction of members of the department of social science of the University of Liverpool confirmed these results. It was found that a relatively high fertility exists among families where the father is " sub-normal " in occupational skill and employability, and in families which are below the " poverty line " and frequently dependent on public assistance. Although the death-rate is higher among families of unskilled workers than of skilled and non-manual workers, their effective fertility remains higher.

Another approach to the problem of the relationship between intelligence and fertility is the direct one of measuring the correlation between children's performance in intelligence tests and the size of the family of which they are members. This has been done, *e.g.* by Bradford (1925), Sutherland and Thomson (1926), and Cattell (1937—using predominantly pictorial tests), and the fact emerges that on the average children of large families are less intelligent than those in small ones. The possibility has been considered that position in the family might affect intelligence, but there is little experimental evidence to support this suggestion. Again, it is suggested that the smaller family might offer more advantageous surroundings ; however, so much has already been said on the comparative constancy of I.Q., in spite of changed surroundings, that it will be realized that such an influence could not appreciably affect the findings. The causal connection undoubtedly appears to be that, on the whole, intelligent parents tend to have small families. There is much evidence that this is not because they are biologically incapable of having more children, but because, for economic and cultural reasons, they choose to have fewer. It is of interest to mention in this connection that Pearson and Miss Moul did not find a correlation of lower intelligence with size of family among Jewish families which they investigated, most probably because among them little restriction of numbers was being practised.

By way of summary, it may be said that (1) there is a positive correlation between higher average score in intelligence tests and " higher " social class as judged by (a) type of school, and (b) parental occupation, and this latter correlation persists even when the children in question have not known their parents ; (2) there is higher fertility among the " lower " occupational grades, where children make poorer scores in intelligence tests ; (3) measuring more directly, there is an inverse relation between high average intelligence and size of family. We have already given the grounds for belief that scores in intelligence tests are fair measures of innate intelligence, and it would thus appear that there are just grounds for believing our national intelligence, interpreted as average I.Q., to be on the decline. The rate of decline is a matter of dispute, and must be considered in relation to another problem no less important and serious—that of the social waste of existing intelligence by denying it the opportunity of suitable education.

This chapter has been confined to a consideration of intelligence and social class. Questions of relationship between such qualities as personality, disposition, etc., and social class are of great interest. But we have seen that tests of personality are not sufficiently advanced to assist in problems either of inheritance or of distribution in a population. As such characters are more dependent on environment and training than is intelligence, we should expect a higher correlation between traits of personality and social class than between intelligence and social class. ✓Self-assertion and qualities of leadership are fostered in the " upper " classes, whereas those who spend their lives in the service of others, those for whom frank declaration of opinions might mean starvation, do not have their assertiveness fostered. With regard to moral qualities, opinions can be hazarded ; but what tests have we ? Perhaps more members of one social class than of others get into prison, but according to the present dispensation of justice one could not always identify law-breaking with immorality. The law is not necessarily founded on a basis of morality : in a recent trial the defendant's confession, " I may be morally responsible but I am not legally so," did not result in conviction. Moreover, different classes receive widely different treatment from the law. (See *Justice in England*, by " A Barrister "—*passim*).

An opinion sometimes expressed is that the differential birth-rate is not a serious matter, as there can be replacement from below by further education of those inferior in intelligence. However, the facts of the previous chapter show that education cannot smooth out differences of intelligence. One frequently hears it said that, although the improvements in intelligence in one generation may not be noticeable, the cumulative improvement over generations may be so. This amounts to acceptance of the inheritance of acquired characters, but, as briefly indicated in Chapter I., this is a theory not generally accepted by biologists. However, as there is much misunderstanding on this subject, it seems desirable to discuss it at greater length in the following chapter.

CHAPTER IX

THE INHERITANCE OF ACQUIRED CHARACTERS

IN Chapter I. brief mention was made of the theory of the inheritance of acquired characters, with a promise to return to the subject in a later chapter. We have now come to the point where its further consideration seems desirable in view of the social importance of its implications mentioned at the end of the previous chapter. The nature of the problem should now be more readily appreciated in the light of our brief survey of Mendelism and of the genetic theory of inheritance. Although our conception of the meanings of the terms has changed since the nineteenth century in the light of increased knowledge, the theory of inheritance of acquired characters is still spoken of as Lamarckism, and the theory of natural selection as Darwinism. The latter term is in a sense a misnomer, for Darwin recognized two causes of evolution, both natural selection and the inheritance of characters acquired or developed by ancestors. He attributed, however, by far the greater importance to natural selection, and this was his great contribution to evolutionary theory. He rejected the extreme Lamarckian view, but did not reject the possibility of the inheritance of acquired characters ; and he admitted ignorance of the causes of variation. Subsequent workers on heredity have provided the evidence which has placed in serious doubt the transmission to offspring of characters acquired by parents during their own lifetime.

Now the theory of the inheritance of acquired characters maintains that effects of environment persist in the hereditary constitution, and that changes induced by environment are handed on to descendants whether or not the environment which caused them remains. There arises immediately the problem of the manner in which the hereditary material could be affected. We have seen that inheritance from parent to offspring is by the transmission of sets of genes in regular positions along the chromosomes. It is difficult to imagine how these genes could be affected by the body, which itself had been affected by the environment, in such a way as to produce in the offspring the effect which the environment had produced in the parents. How, for example, could an excessively large body produced by special feeding influence the size-determining genes in the gametes? A simultaneous effect on the body and on the genes seems equally unlikely; exercise can develop a muscle, but it is hard to envisage how this exercise would so alter the genes of the sex cells that they would determine greater size in the offspring. The alteration of genes (mutation) already described is rare and sudden, and has no known adaptive relationship to the environment. However, the inheritance of acquired characters cannot be dismissed simply because the mechanism of transference is at present inconceivable, for we cannot say that it is theoretically impossible.

The environment undoubtedly exerts a very great effect on the individual: the genes allow much latitude in development. Many features of the developed organism are observed to be due, in detail, to the directive influence of the environment. The dependence of genes on environment has already been discussed in Chapter IV. The hereditary transmission is such that it provides the tendency to develop in a particular way in given circumstances, and in other ways in other circumstances. Functional adaptations can thus be explained—to some extent, though not completely—in terms of cause and effect within the individual.

The work on pure lines quoted on page 122 is evidence against the inheritance of the environmental effect, for it was seen that the differences in size within a pure line, which are due to environmental influence, are not inherited.

Many experiments designed to investigate the effect of environment on successive generations have given negative results; attempts to induce changes have failed, and experiments have shown that the environment has not affected the hereditary material. It is of interest to recall the great resistance of gene material to environmental effects, suggested by the transmission through many generations of "hidden" and apparently unchanged genes for recessive characters.

Some of the experiments just mentioned have dealt with the inheritance of mutilations. Weismann, whose work on the continuity of the germ plasm did much to clarify the position concerning acquired characters, cut off the tails of many successive generations of mice, without any effect on the tail development of their descendants. Presumably the mice, not having tails, could not use them and one would expect—according to the Lamarckian theory—some effect on their descendants. The effects of accident, then, are not inherited—

" wooden heads are inherited but wooden legs are not." Stories of children showing scars in the same position on the body as their fathers' war wounds are fantastic. There may be isolated instances of similarity between the father's scars and the child's birth-mark, which are mere coincidences. Customs such as feet binding in Chinese women have had no hereditary effect, nor has circumcision. The hope that, on account of Lamarckian transmission, such operations as the removal of tonsils or appendix will become unnecessary is illusory. Other instances could be cited to indicate the resistance of the hereditary material to environmental influence. One researcher bred more than sixty generations of flies in the dark, but their power of response to light remained unchanged. Nageli took Alpine plants and cultivated them in the Munich Botanic Garden. Many of them so changed in appearance as to be almost unrecognizable as the same species ; their descendants in the garden similarly differed from the Alpine ancestors. However, there was ample evidence that the changes were due to the influence of the environment *in each successive generation*, for when the plants were taken from the rich soil and milder conditions of the garden back to the poorer soil and other conditions of their Alpine situation, their original characters reappeared : the potentiality to develop them had remained unchanged throughout years of life in the Botanic Garden. Similar results have been obtained with a number of other plants. In the extensive work that has been done to investigate the Lamarckian principle there have been many false alarms, many instances of supposed Lamarckian transmission, where, however, the facts could be explained otherwise, frequently by natural selection. In explaining by selection there is no need to go beyond our knowledge and the observed facts. Nevertheless we must remember that therein there lies no explanation of the origin of the differences—they remain the inexplicable mutations described in Chapter III. It was seen that although some extreme treatment can produce mutation—or at least make it more frequent—there is no evidence of the adaptive nature of the mutation produced.

One "false alarm" concerned "waltzing rats." When rats are rotated on a table at a high speed for a long time a "waltzing" habit is induced. It was claimed by one experimenter that the habit thus induced was inherited. However it was later found that the waltzing habit is associated with bacterial infection (the infection is probably facilitated by decreased resistance due to rotation), and the infectious disease is "caught" by subsequent generations.

An example of apparent Lamarckian transmission where, however, the facts can be explained by selection, concerns the transference of wheat from one climate to another. Grains from wheat grown in Scandinavia were sown in Central Europe, and when after a number of generations the wheat was taken back to Scandinavia, it was found to germinate earlier than did its ancestors taken from Scandinavia. Lamarckians might attribute this to the inherited effect of the warmer climate in producing earlier germination. However, selection offers a more reasonable explanation, and one for which there is some evidence. In the colder climate the earlier shoots tend to be nipped by frost, and late germination is an advantage, whereas in the more southern climate those germinating early have the advantage, and, crowding out the others, become more numerous than they.

Natural selection would thus favour early germination in one generation, and in so far as this variation was heritable the advantage would be perpetuated, and the proportion of early sprouting plants increase in succeeding generations. On return to Scandinavia the wheat would appear as an earlier sprouting type. The early frost would again act as a selection agent, and as the wheat would presumably still be a mixed type the later germinating ones would tend to be preserved.

Not all cases of progressive change in succeeding generations can, however, be explained by selection or by infection in successive generations. Perhaps the working of selection or of some other agent is so subtle that it is not recognized ; perhaps Lamarckian transmission does sometimes occur, but so slowly that practically every attempt to investigate it gives a negative result because the changes during the short experimental period are too small to be measurable.

With regard to mental characters, instincts are sometimes popularly thought of as hereditary habits and memory. There is no more foundation for this view than there is for the Lamarckian principle in general. Moreover, Lamarckian transmission definitely could not explain the instincts, for example, of worker bees, as they do not reproduce and are descended in each generation from non-workers which behave very differently.

A nineteenth-century writer, J. M. Guyau, interested in moral education, spoke of our hereditary tendencies as " nothing but acquired habits," and stated his views thus : " Every individual, by the series of acts constituting the framework of his life, and ultimately co-ordinating themselves for his descendants in hereditary habits, exerts a ' moralizing ' or depraving influence over his posterity, just as he has been 'moralised' or depraved by his ancestors." This is a complete and unquestioning acceptance of Lamarckism. Unless Lamarckism is a reality—and we have seen that it is an extremely doubtful doctrine—it is meaningless to speak of habits ingrained by generations of ancestors.✓ Habits are developed by individuals, and they may be learned by imitation in succeeding generations. There is no ground for believing that the habits—good or bad—of our ancestors affect us except in so far as they affect the *tradition* which we inherit. Inheriting a tradition is very different from inheriting genes. A man may profoundly influence his generation and affect the external heritage of tradition of many succeeding generations, but his work cannot—as far as we know—affect the genes even of his own son if he has one.

The work of the Russian physiologist Pavlov on higher reflex actions is of interest in this connection. Reflex actions can be classified into two main groups, which Pavlov called unconditioned reflexes and conditioned reflexes. The former group of reflexes was so called because of their independence of, or slight dependence upon, the environment. Definite unconditioned reflexes appear in every normal member of a species; they may develop late or perhaps disappear after a certain age, but their course is similar in all members of a species, and they may be said to be hereditarily determined. Some such reflexes are simple, like the well-known knee-jerk in man. Others are more complex, and may actually be combinations of several reflexes. The other large group, consisting of conditioned reflexes, has been the subject of much experiment in Pavlov's laboratories, particularly in connection with the secretion of saliva. Any dog secretes saliva when food is put into its mouth, but some particular dog may secrete saliva when it sees the plate it feeds from, or the person who habitually feeds it. Such a response is acquired by an individual as a result of experience, and is a "conditioned" reflex. A conditioned reflex can be established, so that a dog secretes saliva, say, at the sound of a metronome or at the sight of a special light. A conditioned reflex is established on the basis of another already existing reflex, which may be an unconditioned one or another conditioned one, and thus it is ultimately based on an unconditioned one. It is established by administering some artificial stimulus immediately prior to or simultaneously with the natural one or the previously established artificial (conditioned) one. If a dog always hears the sound of a metronome simultaneously with its reception of food, it will in time expect food—as evidenced by the secretion of saliva—on hearing the metronome, even if no food is given. Pavlov used the term "conditioned" reflexes to indicate their dependence on external conditions. Some particular conditioned reflex may be acquired by but one individual of a species, or by several, or many subjected to the same conditioning influences ; it may even become common to a whole species, although in each case it is individually acquired and not hereditary. It may be difficult to distinguish between so universal a conditioned reflex and an unconditioned one. An example will illustrate this. Five puppies were taken at an early age from their mother and fed on milk. They were used for experimental purposes in the establishment of conditioned reflexes, which developed normally and quickly. One puppy secreted saliva, as if milk had been placed in its mouth, when it saw a continuous red light, another at the sight of a rhythmic white light, the third with the touch of an induction coil, the fourth with the sound of a metronome, and the fifth at the smell of camphor. They were not allowed any other food than milk, and were kept from contact with other animals. After a few months the puppies were shown, but were prevented from smelling, a variety of objects such as pieces of rubber and match-boxes ; among them were pieces of meat and other food-stuffs with which their ancestors were well acquainted. None of these objects, not even the meat, produced in the puppies any salivary activity. The experiment was repeated, allowing them to smell but not to see the objects, and again, allowing them both to see and smell, but in each case with the same result. None of the food-stuffs produced salivary activity ; they had no more effect on the puppies than had pieces of wood or glass until they had once tasted them. This serves to show that the reflex action of secretion of saliva on the sight and smell of meat and other foods, although apparently common to all normal dogs, is not an unconditioned or inborn reflex, but a conditioned one, acquired by each individual. It is also most interesting from the point of view of the study of inheritance. The ancestors of the dog have been carnivorous for countless generations, each normal individual of each generation having acquired the salivary reflex at the sight and smell of meat, and yet this reflex has not become hereditary.

Pavlov set going experiments to investigate further the possible transmission of conditioned reflexes or of any increasing facility for their acquirement. He reported to the International Congress of Physiology in 1923 that there appeared to be evidence for increased facility for developing conditioned reflexes among the descendants of animals which had acquired them. He trained mice to come for food at the sound of a bell; they required many lessons, but their descendants in successive generations required fewer and fewer. However, a few years later, he issued the warning that the experiments had proved complicated, uncertain, and difficult to control, and left open the whole question of hereditary transmission. Further investigation suggested that the improvement was due to imitation, or some kind of communication between successive generations, which was difficult to detect and to eliminate in experimental procedure.

Communication between animals is often of a remarkable nature. One instance may be quoted as an example. A research worker (Eimer) wanted to obtain for dissection a large number of sparrows. He constructed for this purpose a trap consisting of a long tunnel bent in such a way that the snare was concealed from the outside. The birds were enticed by food to go along the tunnel, and were caught at the end—no bird ever returned from the end of the tunnel. The first year Eimer caught a large number of sparrows, the second year only seven young birds, and the third year none, although the sparrows were presumably plentiful each year. This cannot be explained by Lamarckian transmission, because the trapped birds did not return to breed. Observation of the birds' behaviour revealed the reason. Eimer noticed that during the second year of his attempt the older birds made considerable noise—apparently a danger cry—whenever they saw young birds approaching the opening of the tunnel, and the young ones usually heeded the warning.

The subject cannot be dismissed without some consideration of M'Dougall's work on rats, which has been continued through eighteen years. The work had already been in progress several years when Pavlov announced his evidence of Lamarckian transmission in 1923. M'Dougall continued undiscouraged, despite Pavlov's subsequent revocation, although his experiments were designed on similar lines. Rats are intelligent creatures, which readily learn from experience and are thus easily trained to perform certain tasks. M'Dougall and his assistants trained them in several tasks. One was to run around in a hollow wheel like a "squirrel cage," jumping an electrified section of the wall, *i.e.* floor. (A squirrel cage is a hollow circular revolving wheel in which the animal must keep on moving in order to avoid its feet being carried around until it is "standing on its head.") This task evoked so much fear as to be unsatisfactory. A second task consisting of a maze with hidden food was also unsatisfactory, as the speed of finding the food depended on the animal's hunger. A satisfactory task, in which the performances of different rats could be easily compared, was one in which the apparatus consisted of a galvanized iron tank 40 in. long, 20 in. wide, and 20 in. deep, with water in it to a depth of 6 in. At one end was a platform raised above the water and reached by sloping gangways. The gangways were approached through two openings, one in each of the partitions which divided the tank longitudinally into three equal parts. The rats were placed in the water at one end and, disliking water, quickly learned to escape on to the platform. One gangway was electrified, so that the rat received an interrupted current which traversed it while any part of it was in the water. This gangway was also illuminated, and the rat learned in time to avoid the bright gangway where it received the current, and to escape by the dim one where there was no current. The initial rats were from a pure-bred standard stock which had been long inbred. Even so there were large individual differences in their facility for learning the task, which showed the necessity for avoiding any selection capable of vitiating the results, and this M'Dougall claimed to have done. After the first generation he divided the stock at random into two groups, one to be trained and the other as a control, and thereafter, although there was not room to keep all that were born, there was no conscious selection. An interim report in 1926, dealing with thirteen generations, gave evidence of the rats' increasing facility in learning their task in successive generations. In the thirteenth generation the training of the tank rats (*i.e.* descendants of trained ancestors) was not carried beyond the 30th day because by that time all except three of the rats, out of a batch of twenty-tree, had learned to avoid the bright gangway and escape by the dim one. The tank rats as a group showed on the 11th day of training a distinct preference for the dim route, which became steadily accentuated from that day onwards. The performance of a batch of control rats of corresponding generation contrasted strongly with this. As a group they showed no distinct preference for the dim route until the 30th day, and even then it was slight, and training was continued.

Biologists will not readily accept a Lamarckian explanation, and much criticism ensued. This was answered in subsequent reports, and the experimental procedure was varied. Altogether, report has been made up to 1937 on forty-four generations, and there has been gradual improvement. Moreover, M'Dougall claims that there is some evidence that before training is begun descendants of trained rats show preference for the dim gangway. It was suggested that the results might be due to accident rather than genetic causes, to chance influences of the surroundings, but the steady increase over generations seems to rule out this objection. There is considerable evidence that the differences in performance between different rats is a function of their genetic composition : there are good performers and poor ones, and cross-breeding gives intermediates. It was *even* suggested that the improvement was due to telepathic communication between the rats and the experimenter, who desired the trained set to do better than the controls. However, neither M'Dougall nor his assistants were conscious of any desire that one group rather than another should succeed, and some tests were carried out by assistants ignorant of the identity of the rats. Actually, handling by different workers is itself a source of error. Pavlov and other researchers have observed that animals react differently to different people. M'Dougall largely handled the trained rats himself, and, presumably, became more experienced in manipulating them, whereas there was more variety in the personnel of the workers with the controls.

A probable explanation offered in criticism was that of communication between mother and offspring. The mother remained with the young up to the end of the fifth or sixth week ; training was begun about the end of the fourth week, by which time rats are capable of vigorous running. Such communication, it was suggested, might be by transference to the embryo of some hypothetical hormone, but this suggestion cannot profitably be discussed without definite knowledge, which is not available. The communication, it was also suggested, might be due to some telepathic impression, or, what is much more probable, to timidity or other emotional state developed in the mother by the training process, and imparted to some extent to her progeny by "sympathetic induction"; or it might be due to actual instruction or warning given by the mother. M'Dougall tried to eliminate this source of error by placing the young of trained rats with untrained foster-mothers. As far as the test went the improvement in successive generations appeared to persist. Moreover, the descendants of trained male as well as trained female parents showed improvement in later generations. It would be interesting to see the results obtained from trained males only; it would seem profitable to investigate separately the offspring of trained females and trained males.

M'Dougall held that there was considerable evidence for regarding the improvement as definitely genetic, and not environmental in any of the ways just described. If genetic, it might be due either to selection or to Lamarckian transmission. Any selection thought likely to influence the results was carefully avoided. It was suggested that selection might be taking place, as the slower rats would be more likely to be killed off by the electric shocks, or perhaps the electricity lessened their fertility, as they would be subjected for longer periods to its influence. Both these suggestions were dismissed because the mortality from electric shock was very low and no reduced fertility was observed. M'Dougall even tried the result of adverse selection. He deliberately chose the offspring of poor performers, but the improvement in later generations persisted. However, some evidence difficult of interpretation arises, inasmuch as the untrained controls themselves were better in later than in earlier generations. This improvement is probably due to unrecognized selection by the experimenter and, perhaps, to close inbreeding. This suggests that these causes may be at least partly responsible for the improvement in the trained stock also.

If the changes are genetic and selection cannot account for them, M'Dougall insists that we must admit the possibility of Lamarckian transmission. If such transmission exists, its nature—whether, for example, it is specific to the situation or concerned with " general intelligence "—and the mode of transmission remain a mystery. Crewe and others have carried out similar experiments, but have not confirmed these results. M'Dougall attributed Crewe's negative results to the fact that the task he set the rats, although superficially similar to his own, must have been considerably easier, as the rats learned it rapidly, some with scarcely any teaching. The greater simplicity was probably due to the smaller size of the tank, its slightly different shape, and to brighter and more contrasting illumination. M'Dougall contended that the difficulty of the task was important, and that positive results could scarcely be expected unless the rats were faced with a task as near as possible to the upper limit of their adaptive power or intelligence, for " the more repetitions there are involved in the learning process the ' deeper ' would be the effect upon the individual learner, and the more probable some transmission of that effect."

Space forbids a more lengthy discussion of the facts. It is to be hoped that M'Dougall's recent lamented death will not put an end to this interesting series of experiments.

The matter is still open, and a verdict of " not proven " must be returned on the validity of the Lamarckian principle. Contradictory results of different workers are a warning : some subtle flaw in M'Dougall's procedure may not have been detected. Many competent judges are sceptical about his work, and it must be remembered that his results are insufficient to weigh against the great mass of evidence unfavourable to the Lamarckian principle. Inheritance of acquired characters has been discussed at some length because of its importance in connection with the biological progress of man : many unjustifiable assumptions are made. It must be emphasized that, even if Lamarckian transmission does take place, it must do so exceedingly slowly. If it took place at even a moderate speed it must certainly have been detected. The forty-four generations of rats in M'Dougall's experiments would represent for human lives about fourteen centuries. It is useless to hope that the Lamarckian transmission of man's efforts will quickly improve a nation : if it does so at all, which is, as we have seen, most doubtful, the process must be exceedingly slow. Selection, favourable or adverse, would in a mixed stock be quicker in its effect. A fact frequently forgotten by unreflecting " Lamarckians " is that a man's achievement extends throughout his life, whereas his children may be born when he is comparatively young.

From one point of view problems of inheritance of acquired characters might be considered relatively unimportant for man compared with other animals, because man has speech, writing, and other forms of permanent tradition—an external social heritage handed on from one generation to another, cumulative in its result and similar to the inheritance of acquired characters. Other animals have their means of communication one with another, and experimenters must needs eliminate this factor, as far as possible, from any experiment to investigate the Lamarckian principle. It will now more readily be understood how much more difficult it is to eliminate or control this factor in any investigations into the inheritance of mental characters in man. No other animal possesses the degree or kind of permanent tradition that man possesses. One man's work, ideas, and ideals—one man's acquired characters—may be handed on in this external tradition, but they are not handed on in the genes ; and some writers take a serious view of the decline in national intelligence, arguing that the decline may become so great that there may eventually be insufficient people capable of understanding the complexity of our civilization—particularly the achievements of applied science—for it to be carried on. It is a consoling reflection that many regard this view as exaggerated and unduly pessimistic.

If none—or very few—of the effects of learning are handed on innately, we may well pause to consider the astounding degree to which we learn from our environment during a lifetime. Man is a very teachable creature. He may have fewer specific reactions than other creatures, but he is more plastic, more educable. In Pavlov's terminology, though he possesses some unconditioned reflexes, the number of conditioned reflexes he has acquired is incredible. Pavlov said, " It is obvious that the different kinds of habits based on training, education, and discipline of any sort are nothing but a long chain of conditioned reflexes." And again, " For man speech provides conditioned stimuli which are just as real as any other stimuli. At the same time speech provides stimuli which exceed in richness and many-sidedness any of the others, allowing comparison neither qualitatively nor quantitatively with any conditioned stimuli which are possible in animals."

Here we see the extraordinary power of education and the extent to which we are dependent on the type of education we receive. Children depend on parents and teachers to initiate them into a tradition. We gain much from good teaching and example and from the inculcation of good habits, and we are put at a great disadvantage by the contrary influences. In games and various acts of skill it is as difficult to abolish many superfluous movements as to acquire the appropriate ones, and with regard to conditioned reflexes it is equally difficult to overcome established negative reflexes, *i.e.* inhibitions.

For a long time psychologists have stressed the importance of early habits. Pavlov's work has shown the greater facility of the young animal to acquire conditioned reflexes. Habits and inhibitions of early days may have far-reaching effects. There may be some connection here with the problem of intelligence and social class. It will be remembered that the influence of environment on the I.Q. has been shown in most cases to be small, and it may perhaps be found to be greater when the influence of environment on the as yet little explored early years is better known ; but so far we have no positive evidence in this direction.

All that has been said about the stimuli of the environment establishing conditioned reflexes must not be allowed to give the impression that thereby all individuals can be made alike. Pavlov's work showed such great differences between individual dogs as have already been stressed in the case of human beings. He found differences in rate of learning and in all reactions, and discovered that different individuals needed different treatment; for example, some nervous dogs could respond only to weak stimuli, and were inhibited by strong ones. His work is of far-reaching importance, as he realized when he wrote, " having acquired some knowledge of its general principles, we feel surrounded, nay, crushed, by the mass of details, all calling for elucidation." Since his death a few years ago the work has been continued in the laboratory specially built for the study of conditioned reflexes at the Institute of Experimental Medicine in Leningrad.

CHAPTER X

HEREDITY AND SOCIAL AFFAIRS

THIS book has been concerned with the differences between human beings, and we have seen that there are between them considerable differences both of degree and of kind. Some of these inequalities can be assigned to the varying influence of environment on individuals whose biological constitution is fairly similar, and even, as in the case of uniovular twins, on those of identical genetic constitution. Other differences are unquestionably due to differences of biological constitution which have been described as gene differences. The necessity for avoiding false antithesis between characters determined by heredity and those determined by environment has already been discussed. Although popularly we speak of the inheritance of a character, we must not forget that what is inherited is a constitution capable of giving a range of characters according to environmental differences. The laws governing the inheritance of these biological differences between men have been considered, and it has been seen that in some cases a definite prediction can be made, with the knowledge of ancestry, from one generation to another. It can sometimes be said with virtual certainty that a given trait will or will not reappear. It can, in other cases, be estimated that there is, say, a 50 per cent chance or a 25 per cent chance that a trait will reappear. From our study of Mendelism it will readily be understood that such predictions can only be made about characters dependent on single genes. It is desirable, in cases where a hereditary defect is known or suspected in self or relations, to consult a medical man, who may be able to give advice on the nature of the trait and the likelihood of its reappearance. A good many hereditary traits are not, of course, commonly recognized or even suspected as such by those possessing them. Clinics and doctors could do service by giving advice, even though unasked. Conceivably the time will come when it will be usual or even compulsory for those contemplating marriage to have not only themselves but their pedigrees examined for possible hereditary defects.

A large number of characters, including almost all mental ones, are dependent, as we have seen, not on single genes but on many, and in these cases nothing certain can be predicted for the individual.

Now these facts about inheritance are important in connection with some often discussed social repercussions of heredity. The question of sterilization of those suffering from certain heritable defects is fairly often discussed. The practice has been legalized in some countries (*e.g.* Denmark and certain American states). In some cases it is imposed more or less as a penalty, in others as a precautionary measure on discharge from an asylum. Frequently the operation is voluntary. The proposed British legislation suggests voluntary sterilization. In regard to mental defectives, how far this can be considered voluntary is questionable. Let us consider the genetic effect of sterilization from the ethically neutral standpoint of science, and not, for the moment, as a question of social policy. If everybody suffering from some dominant defect such as symphalangism were rendered sterile, then by that action on a single generation[1] the defect would be wiped out, apart from its possible reappearance by mutation. For if a dominant trait of this kind is present, it declares its presence, and no one can carry it unknown, and, if no one possessing it reproduces his kind, the character disappears. However, many traits almost certainly to be considered dominant fail to show on account of some variation in the internal or external environment (*cf.* page 94). Such traits would be difficult to eliminate. With regard to sex-linked characters, of which Leber's disease (optic atrophy) is generally considered to be one, " If all persons suffering from Leber's hereditary optic atrophy were sterilized, we could eliminate the incidence of the disease in the female sex completely in one generation and reduce its incidence in the male sex by 50 per cent. in each generation thereafter " (Hogben). This is so because a woman who shows the disease must be homozygous for it, and must, therefore, inherit the gene from both parents. After the sterilization of all possessing the trait she could never get the gene from the male side, as it would be apparent in all males possessing it, and they would be already sterilized. The sterilization would not be carried out in " carrier " women, in whom the gene would not be recognized, and they could hand on the defect to either sons or daughters—the latter would be carriers, the former would show it, and on the average there would be equal numbers of sons who inherited the gene and who did not inherit it (*cf.* the pedigree on page 98). If, however, everybody suffering from a recessive trait such as deaf-mutism were sterilized, the defect would not immediately or even quickly be wiped out, for many people would be carrying it unrecognized. If the process were repeated in successive generations the trait would become progressively rarer, but the reduction becomes progressively much slower in subsequent generations as the trait becomes rarer. The amount of reduction depends on the rarity of the trait in the population. An example from Hogben may be quoted, "The actual incidence of albinism is less than 0.01 per cent, probably about 0.005 per cent. If sterilization of all albinos were carried out in every generation, it would require a period about equivalent to the Christian era to reduce the incidence of albinism to one-half of its present dimensions. On the other hand, if all persons suffering from *diabetes insipidus* or split foot[1] were sterilized, these conditions would be obliterated in a generation." J. B. S. Haldane, who has done much original work on selection, speaking of ordinary recessive traits, says, "When we come to ordinary recessives we can say at once what the effects of sterilization would be. Except in cases where, as with deaf-mutism, there is a tendency for recessives to interbreed, there would be no noticeable effect in less than thirty or forty generations."

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[1] In the sense of those existing at a given time, as generations overlap.

It is seen that the elimination by sterilization (or by otherwise preventing reproduction) of a character dependent on a single recessive autosomal[2] gene may be a very lengthy business. It will readily be understood that the attempt to eliminate similarly a character dependent on several or many recessive genes would be even slower.

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[1] *i.e.* dominant traits.

[2] *i.e.* in an autosome (a chromosome other than an x or y chromosome). *Cf.* page 67.

This fact constitutes a serious setback to the hopes of those who propose to eliminate mental defect by the sterilization of mental defectives ; for, as it was stated in Chapter VI., hereditary mental defect is of different kinds, all pretty certainly dependent on several or many genes in general of a recessive nature. Moreover, the environmental causes of mental defect are as yet little understood, and may be shown to be more extensive than they are at present known to be. It is pretty certain that environmental influences such as birth injuries are responsible for some defects. The fact that the defective known as the Mongol idiot occurs more frequently among children of older mothers, many of whom have already borne a number of normal children, suggests a pre-natal environmental factor which may itself be to some extent hereditarily determined. Thus we see that with dominant traits—particularly those showing themselves early in life and those not liable to skip a generation—and with sex-linked ones, a quick and measurable reduction in incidence can be expected as the result of a policy of sterilization. In a case of single autosomal recessives and characters dependent on several recessive genes we see how little reduction can be achieved. For example, in the case of mental defect no doubt sterilization would reduce its incidence, but would do so exceedingly slowly and with the sacrifice of potential children who might be normal. There are those who contend that what little can be done should be done. With regard to the potentially normal children of mentally defective parents it can, of course, be urged that the defective parent provides a very poor environment. However, many objections are raised against sterilization. Some object, fundamentally on moral or religious grounds, to what they consider an interference with nature, others to what is unquestionably an interference with liberty. Many oppose the legalization of sterilization because they mistrust the judgment of those who might be empowered to decide where the line should be drawn between those who are " fit " and " unfit " to procreate, and in general they are apprehensive about a misuse of the practice. Some existing laws go too far and suffer from an indefiniteness which makes interpretation too much an individual responsibility. There has been—in countries where it is legalized—recommendation for sterilization of those whose defect was economic rather than biological and hereditary. Social distinctions and class privilege are almost certain to be involved in judgment of social inadequacy in capitalist states, where the rich can shelter and protect the biologically inferior members of their families, whereas the poor cannot so easily do so. Many think that the legalization would tend to discourage salutary research into the environmental causes of mental defect. Segregation of mental defectives in institutions has much to recommend it. It is more likely to prove acceptable as an immediate policy, while the controversy over sterilization continues. It would relieve the home and community of the presence of defectives in their midst, and for the defectives themselves it would provide a suitable environment and training. Higher grade defectives are capable of much socially useful work : they are capable of a good deal of monotonous work without boredom and without the distraction caused by other interests. The present provision of institutions is gravely inadequate. There is probably need for about four times as much accommodation as exists. The whole problem of mental defectives and the mentally dull is in urgent need of attention. The presence of dull children is a handicap to other pupils and to the teachers. Some schools in very poor areas have a larger proportion of such children than more fortunate schools, so that the brighter children are handicapped.

An aspect of the social selection problem, about which one hears perhaps more than about any other, is the consequences of the differential birth-rate. This was mentioned in Chapter VIII. in connection with the problems of the inheritance of intelligence and the correlation between intelligence and social class. Facts mentioned in the present chapter have their bearing also on this problem—they remind us that the rate of adverse selection may not be as rapid as some pessimists would have us believe. J. B. S. Haldane has worked out approximately the rate of working of what he calls " slow selection," which occurs owing to differential fertility, and to mortality due to characters dependent on single gene changes and on multiple factors. His work (and that of R. A. Fisher and others) emphasizes the need for knowledge of the mode of transmission of the hereditary character (*i.e.* whether dependent on a single gene or on several, whether recessive or dominant) before any prediction can be made about the influence of selection due to a differential birth-rate or other cause. We also need more knowledge concerning mutation and mutation rates in man. There must be reappearance of traits by mutation. There must be considerable *natural* reduction of a trait such as hæmophilia. According to Haldane, hæmophilics beget on the average less than a quarter of the number of children produced by their normal brothers—in fact, probably a quarter of all hæmophilia genes in the population are wiped out in each generation. "Unless, then, there were some source from which they can be replaced, the frequency of hæmophilia would be diminished by 25 per cent. in each generation, and by a simple calculation from the existing frequency of hæmophilia it could be shown that at the time of the Norman Conquest the entire male population of England must have suffered from hæmophilia. We have reason to believe that this is inaccurate. We therefore look for some evidence of the origin of new hæmophilia genes." The evidence comes from the consideration of pedigrees where the defect has undoubtedly arisen as a mutation.

From our knowledge of the inheritance of mental characters—of mental defect and of intelligence (admitting that we do not really know what this is)—it would appear that the processes of selection going on among the people of our country are such as to lead to an increase in mental defect (*cf.* page 127), and a decline in the average national intelligence (*cf.* pages 165ff). Cattell, the author of *The Fight for our National Intelligence*, is among those who take a very serious view of this decline, and he estimates it as an average fall in I.Q. of one point per decade—" a decline," he says, " which can only be described as galloping." He adds, " It is no comfort to reduce this to absurdity by continuing the calculation backwards for a few hundred years, for the differential birth-rate is a social innovation of the last fifty years. Conversely, there is no particular terror in the calculation that at present rates half the population would be mentally deficient in three centuries. For grave social and economic consequences would ensue long before then which would end or mend our society."

It is difficult to make predictions about the quantity or quality of populations, but just as there is fairly general agreement that, if the present tendencies continue, our country will reach its maximum population about 1940 and thereafter decline, so it is pretty generally agreed that the quality of the population is changing in a definite direction. J. B. S. Haldane estimates that, if the present differences in fertility between the social classes continue, we may expect a slow decline, perhaps of 1 or 2 per cent per generation, in the mean intelligence quotient of the population, which, although not as great as Cattell's estimate, is, Haldane admits, on the whole deplorable. The differences in fertility may not continue. It is interesting that in Holland, where there is no government check to the spread of knowledge about methods of birth control, the differences in fertility have largely disappeared. Moreover, social legislation designed to alleviate the financial burden associated with the education of intelligent children, and greater social equality, may play their part in checking the progressive fall in average intelligence. In this connection the need for family allowances and really helpful income tax benefits should be considered, and it should be remembered that the present organization of society in this country tends to penalize, as potential parents, the " middle classes " in comparison with the rich and poor. Another social and economic problem which should be reviewed in this connection is the employment of married women. It is undesirable that intelligent women should remain unmarried and childless because they cannot afford to marry. Here again the " middle classes " are penalized. Few seem to object to wealthy women spending their time on committees or in other social activities while their homes and children are cared for by paid employees. No one, apparently, objects to film stars and other actresses continuing their work after marriage. It is also a common practice among the poor for married women to work, and in some cases their children are cared for in day nurseries and nursery schools. The outcry against " two incomes in one home " is raised only where the " middle classes " are concerned. In a country where there is no attempt to equalize incomes, or to adapt them either to needs or to work done, such comments reveal either stupidity or hypocrisy. A society which believes that " a woman's place is in the home " should not make it necessary for a widow with young children to earn their livelihood instead of taking care of them at home.

At present there is a progressive " sterilization "—at least a cutting down of the fertility—of those possessing the qualities which make for success in life. In fact, not only at present, but also in other times and other civilizations, some of those possessing the qualities most admired were least fertile. The celibacy of priests and the sending forth of strong men to battle have been causes of this relative infertility, this contradiction between biological and social success, but it was insufficient, at least in comparison with present tendencies, greatly to alter the quality of populations. The present so-called educational equality of opportunity merely serves, in the absence of social equality, to aggravate the trouble ; it is dysgenic. By means of scholarships many intelligent members of the poorer classes can rise in the social scale and so enter a class which is less fertile, *i.e.* in which it is common to marry later and have fewer children. How much of this lessened fertility is due to choice and is a matter of tradition and necessity for social advancement, how much due to biological causes, is a matter of dispute, but there is considerable reason to believe that it is largely voluntary ; a dependent family may be a handicap to a man who wishes to climb. There is nothing in these facts which should lead to a diminution in the effort to obtain equality of opportunity. The effort should be to increase it, to make it more real, so that social advantages shall not have precedence over real merit. We might then find the most intelligent people in posts requiring intelligence, irrespective of social origin. It ought to be possible to " rise in the world " without the sacrifice of early marriage and children. It would be interesting to know the state of affairs in the U.S.S.R. ; an investigation of the correlation between intelligence and size of family there would be most illuminating. Democracy and a wide social ladder are sometimes criticized as leading to biological segregation, but this would not have serious social consequences if there were not a differential birth-rate. The organization of society in Russia may lead to a different kind of stratification with an aristocracy of brain, and, if so, it will be interesting to see how far it is hereditary. The point of view is sometimes expressed that, after all, the qualities making for success are largely aggression, greed, self-seeking, and love of power, and if these are hereditary it is all to the good that the successful are less fertile. In a civilization where pandering to the popular taste is so rewarded that a film star earns vastly more than the most brilliant scientist, where a great artist is rarely recognized until after his death, and where financial success is valued so highly, some would ask if it really matters that the successful tend to commit racial suicide. However, the undesirable qualities of those who have " arrived " are probably traditional and acquired rather than innate. The view that if there were fewer scholarships and less chance for the poor to rise in the social scale the intelligent would remain to leaven an "inferior" class, and that the intelligent poor with no opportunity to rise are a safeguard for the reserve of intelligence in case of social need, is too contemptible to merit further consideration.

Reference was made in Chapter VIII. (page 162) to the work of Gray and Moshinsky published in the *Sociological Review* in 1935. They made inquiry into the relationship between ability and opportunity. They tested a representative sample of over ten thousand children between the ages of nine and twelve and a half years attending elementary (including central), secondary, private, and preparatory schools in the London area, using Otis intelligence tests adapted for English children. It is impossible here to give a detailed analysis of the work, or an adequate impression of the quantitative nature of it. Some astounding facts emerge; for example there are in London "more able children in central schools than in all fee-paying schools put together. Yet practically none of these have the opportunity of entry into the professions and the higher ranks of the business world enjoyed by those who attend secondary or public schools." Few children whose parents are able and willing to pay school fees are deprived of the opportunity of higher education, though their ability may fall far short of that demanded for secondary school entrance. Whereas "it is almost impossible for a less gifted child of the working classes to scrape into the ranks of the highly educated." Many able children of the poorer classes qualify for secondary school entrance, and even win scholarships, which they refuse. On the "Honours List" in their elementary school their names appear with the melancholy legend, "Scholarship not taken up." When comparison is made of the opportunities enjoyed by equally able children, say by those reaching the levels of ability touched by the superior 50 per cent of all fee-paying pupils, then it is found that seven fee-paying pupils receive a higher education for every one free pupil of equal ability. Moreover, a child of inferior ability born of wealthy parents has more than a hundred times the chances of receiving a higher education possessed by a correspondingly dull child of poor parents. Another aspect of opportunity and ability that would be worth investigating is the relationship of I.Q. to A.Q. (achievement quotient)[1] for different types of schools—it would most probably be found to vary according to quality of teaching and size of classes as well as home environment. In view of the enormous "waste" of intelligence which the above-mentioned discrepancies in opportunity indicate, concern about decline in intelligence seems somewhat hypocritical. Why should decline in intelligence be bewailed by those who would deny the intelligent the opportunity to use their intelligence in the higher professional callings? There are many who seem to fear equality of opportunity. If they were secure in their feeling of superiority they would not fear competition. Such people do harm rather than good to eugenics propanganda and lay it open to such charges as the following: "The term eugenics has become identified with ancestor worship, anti-semitism, colour prejudice, anti-feminism, snobbery, and obstruction to educational progress" (L. Hogben). In a work, *The Family and the*

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[1] By using tests of various school subjects it is possible to assign to a child an "educational age." The achievement quotient (A.Q.) is obtained by dividing the educational age by the mental age.

Nation, by W. C. D. Whetham and his wife, we find the following : " Scholarships have their dangers when used to raise those who win them too suddenly and completely out of their *natural class*."[1] What, we may well inquire, is a man's " natural class " ? Elsewhere we read, " It is probable that the policy of competitive examination, when driven to excess, has resulted in closing partially the doors of various honourable professions to those who, in due course of time, would have been best fitted to excel in them." If this were merely a lament that the competitive examinations gave the advantage to those with the wrong qualities irrespective of class, that it favoured, say, precocity of development instead of real ability, it would be quite an innocuous statement, but its context is : " During the last two centuries, the landed and official classes could be certain of obtaining for many of their sons posts in which, at all events, a living wage was secure. Now the posts are filled by competitive examination from a much larger field." Why should the sons of the landed and official classes be *ipso facto* " best fitted to excel " in the various " honourable professions " ? In the same work we find also the following : "The overcrowding of certain professions and careers, which without doubt has occurred in recent years, may be due partially to certain faults in our recent methods of education. Both our public and elementary schools have been much to blame, the one in that they failed to modify the type of education to suit the altering conditions of national life, the other that they tended to depreciate manual activity and craftsmanship, and over-supplied the ranks of the clerks and penmen. The great public schools go on training their boys chiefly in classics and ancient literature, when the demand has been for men of general education, for men of science, for economists, engineers, and scientific agriculturalists, of the same class and breeding as the men supplied by the public schools. The classically trained men have difficulty in finding openings in after life, owing to their type of education. The men educated scientifically in schools of other types are often rejected because their *heredity*[1] and training leave them *unfit to deal with men, especially with workmen, foreigners, and natives.*[1] Moreover, from the employer's point of view they often lack the guarantees of character and the intuitive sense of masterfulness that are the usual concomitants of the man of good family."

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[1] The italics are mine.

We need to know a good deal more about the inheritance of character, and of a contradictory nature from that which we already know, before we can admit that "the men educated scientifically in schools of other types" ought to be rejected because their *heredity* as well as their training leaves them "unfit to deal with workmen, foreigners, and natives." All the three extracts quoted show confusion between biological and social inheritance.

Galton should be appreciated for the value of his work, but we must admit that its influence on the development of studies of human heredity was prejudicial to the progress of experimental genetic studies. His followers have accepted and accentuated his aristocratic bias. In a sense, however, one might say that he gave the "upper classes" enough scientific rope to hang themselves; their claim to superiority in innate ability has encouraged inquiry, and now that the problems of inheritance of ability are seen in a clearer light, the inheritance of tradition is more

[1] The italics are mine.

easily distinguished from the inheritance of genes than it was in the days when *Hereditary Genius* was written. In so far as there are clear-cut distinctions between the social classes, they are not differences of intelligence but of tradition and behaviour. It is true that there have been found *average* differences in test intelligence between the social classes. These have been commented on in Chapter VIII., and attention has been drawn to the overlap between the groups and the complete range of intelligence in all of them. The overlap is probably even greater and the average differences less than has appeared, as the tests may not have eliminated the environmental factor of the advantage enjoyed by the children of the cultured home in dealing with some of the tests (*cf.* Chapter VII.). The work of Gray and Moshinsky, mentioned on page 162, indicates the caution necessary in generalization even about averages, for there appear to be occupational groups of different average within the larger groups. A group fairly homogeneous in social tradition is far from homogeneous in intelligence, whereas certain characteristics of behaviour may be considered as practically discontinuous between the groups. Consider speech, accent, table manners; in these "East is East and West is West"—the *habitués* of the East End tavern and of the Ritz have each their own traditional behaviour. These differences in tradition are not innate, but acquired, as are the vast differences in behaviour between ourselves and our fiftieth great-grandparents. Shaw's *Pygmalion* is a parable for misguided eugenists. A very great difference between the social classes in this country is speech. Broadcasting may do something to alter this state of affairs, but just as one does not learn to play football by watching the game every week, but by playing, so one cannot learn good speech simply by hearing it, but by living in an environment where it is habitually employed. Compulsory education has made a difference. All may learn to speak " educated English " (not necessarily " standard English "), but the educated do not in England form a " social class." Even a high degree of education is not itself enough to admit a man to certain social groups. " Standard English, on the other hand, is a class dialect " (Firth). This vague " standard English " is also referred to as " good English, well-bred English, upper-class English." In the Pronouncing Dictionary Jones says, " it is usually heard in everyday speech in the families of southern English persons whose menfolk have been educated at the great public schools." A reluctance to alter one's speech must tend to perpetuate class differences, and there must be many who speak " standard English " yet do not wish others to speak as they do, for their feeling of superiority would then disappear. Modes of speech are not inborn; there is no evidence, or probability, that a French child brought up in England to speak English will afterwards learn French any quicker than an English child would. Any type of speech can be learned, and these speech differences which at present are the cause of prejudice and misunderstanding are not likely to persist in their present form, for, with increased facilities for education and greater equality of opportunity, educated and intelligent people, as distinct from the mere speakers of " standard English," are more likely to secure the positions of authority.

Pavlov's work and other researches have shown how great are the possibilities of training—particularly in man, the most educable of all animals. Man, moreover, differs from other animals in his mode of thought; he has a type of reasoning—a power of forming concepts—which they do not possess ; he can modify his conduct in the light of experience and in the light of ideals to a very high degree. Education and environment for him become of extraordinary importance. Environment can effect great changes in behaviour in the individual and great similarities between individuals. Although it cannot, as we have seen, equalize intelligence, it can in some cases affect intelligence.

A great deal has been written in this book about intelligence, but the importance of acquired knowledge must not be underrated. Intelligence is certainly not all that matters in a civilization. The growth of civilization has depended on the intelligence of comparatively few ; the characters of nations have depended on a few leaders, the rest have followed. The complexity of a civilization may increase without any change in man's innate intellectual endowment. Even many educated people only "think for themselves" within the limited sphere in which they are trained. Those of little intelligence are almost incapable of valid generalization and are more dependent on the specific habits they learn. The use to which intelligence is put matters greatly. Intelligent people may spend their time on worthless or harmful pursuits ; swindlers may have very high test intelligence. People must be taught how to use their intelligence, and learn to develop good habits and desirable social behaviour. These are problems of education. The genetic basis of behaviour is a subject on which much research is still needed. The psychological (environmental) aspect has been much more thoroughly explored.

It may then be said that our biological knowledge is sufficient to tell us that men are not born equal in endowment, or, to speak more accurately, babies are not born equal in their potentialities for development. Advocacy of equal opportunity and equal rights is and has been for its enlightened protagonists a protest against class privilege. They do not believe that education and training could ever be equal for all, partly because home influences could never be completely equalized, and human psychology is such that parents desire more for their own children than for others'. We have seen that, in so far as equal training can be achieved and its effects on different individuals observed, there results no smoothing out of differences in ability : people profit from their education in proportion to their educability. A rich environment means nothing to an idiot. Environment and training must be adapted to the individual. In the past they have been largely adapted to the social classes, within each of which we have seen that there is a full range of intelligence which largely determines educability. *The known biological facts support neither a rigid class system with hereditary privilege nor the belief nourished by some that education can make all men equal.* If the environment were more nearly equal for all, if social conditions were vastly improved for a very large section of the community, we should have more chance of finding out which inequalities between men were due to differences in environment and which to heredity.

An attempt has been made to survey many problems. In covering so much ground the consideration of social implications is necessarily restricted. If knowledge of the facts set forth in the earlier chapters could have been assumed, this final chapter might have been enlarged tenfold. As it is, the social implications of the facts of inheritance have been merely foreshadowed. In conclusion it may be said that much research is still necessary, not only into many problems of human biology and inheritance, but also into the relationship between these and social problems. The application of biological facts to economic and social policy is exceedingly difficult and has often led to untenable generalizations being made, whereas it should be admitted that our knowledge is as yet insufficient to justify them.

FURTHER READING

A FEW SELECTED BOOKS

CATTELL, R. B., *The Fight for our National Intelligence.* (P. S. King.)

GATES, R. RUGGLES, *Heredity in Man.* (Constable.) A Reference Book.

GRAY, J. L., *The Nation's Intelligence.* (Watts.) This book stresses a different aspect of the problem from Cattell's.

HALDANE, J. B. S., *Heredity and Politics.* (Allen and Unwin.)

— *The Inequality of Man.* (Pelican.)

HOGBEN, L., *Genetic Principles in Medicine and Social Science.* (Williams and Norgate.) Parts are difficult to follow without some knowledge of mathematics.

HUXLEY, J., *Essays in Popular Science.* (Pelican.)

HUXLEY, J. S., and HADDON, A. C., and CARR-SAUNDERS, A. M., *We Europeans.* (Jonathan Cape, and Pelican.) A discussion of "Racial" problems.

JENNINGS, H. S., *The Biological Basis of Human Nature.* (Faber and Faber.)

SINNOT, E. W., and DUNN, L. C., *Principles of Genetics.* (M'Craw-Hill.) A useful general textbook.

Various works of less general interest have been mentioned in the text. Much of the work quoted in the course of the book has appeared in various journals. An extensive bibliography of such articles is given in *Heredity and Environment,* by Gladys C. Schwezinger. (Macmillan.)

GLOSSARY

Achievement quotient. Educational age divided by chronological age. See page 201.

Acquired character. A character developed in an individual in response to environmental conditions.

Adrenal gland. One of the endocrine glands. See page 81.

Allelomorphs. A pair of genes occupying corresponding *loci* in homologous chromosomes. Sometimes used of the pair of characters associated with these genes. See also " multiple allelomorphs."

Autosome. A chromosome other than an x or y chromosome. See page 67.

Biometrics (*or biometry*). A science based on the measurement of living things. See Chapter VI.

Carrier. In this book used in the sense of an individual carrying a recessive gene whose presence is masked by the effect of the dominant allelomorph.

Cell. The unit division of the protoplasm of a plant or animal body.

Chromatin. The deeply staining substance of the chromosomes.

Chromosome. One of the paired bodies which are apparent in the cell prior to cell division, and which stain deeply with certain dyes. They bear the genes.

Coefficient of correlation. See page 113.

Complementary factors. See pages 74–77.

Conditioned reflex. See page 176.

Continuous variation. See page 103.

Crossing over. The interchange of corresponding parts of homologous chromosomes.

Cytoplasm. The extra-nuclear protoplasm.

Diploid individual. One which develops from a fertilized cell, and whose cells have thus the double number of chromosomes.

Discontinuous variation. See page 103.

Dizygotic twins. Ordinary fraternal twins developed from two fertilized eggs.

Dominant character. One which expresses itself whether the determining gene be in the homo- or the hetero-zygous state. With complete dominance the recessive character is apparently hidden. In incomplete dominance it is not so, and the heterozygous form differs in appearance from the homozygous.

Ductless (or endocrine) gland. See page 81.

Educational age. See page 201.

Endocrine (or ductless) gland. See page 81.

Factor. See " gene."

Fertilization. The fusion (union) of male and female gametes.

Filial regression. See page 111.

Gamete. A reproductive cell of either sex.

Gene. A hereditary factor carried in a chromosome.

Genetics. The study of variation and heredity.

Genetic variation (or genetic difference). Variation or difference due to changes or differences in the genes (*i.e.* in the hereditary constitution of the individual).

Genotype. The hereditary constitution of an individual, its factorial or genetic composition. See page 44.

Haploid individual. One possessing a single chromosome from each homologous pair. Gametes are haploid.

Heterozygous individual (or heterozygote). One which in respect of any pair or pairs of genes contains opposite not identical allelomorphs.

Homologous chromosomes. The members of a corresponding pair of chromosomes derived from the two parents respectively.

Homozygous individual (or homozygote). One which in respect of any pair or pairs of genes contains identical not opposite allelomorphs.

Hormones. Secretions of the endocrine glands.

Intelligence quotient (I.Q.). Mental age divided by chronological age and multiplied by 100 (*i.e.* expressed as a percentage). See page 135.

Lethal factor. One which when present in the homozygous state produces such extreme modification of the organism that death ensues.

Linkage. Tendency for genes to remain linked in their inheritance and not to segregate independently because they are carried in the same chromosome.

Meiosis. Nuclear division which results in halving the number of chromosomes. Sometimes termed " reduction division."

Mental age. See page 135.

Mitosis. The normal process of division of the cell nucleus whereby the number of chromosomes is kept constant.

Mode (*or modal value*). See page 107.

Monozygotic (*or uni-ovular*) *twins*. So-called " identical twins." They are developed from one fertilized egg which splits into two soon after fertilization.

Multiple allelomorphs. Members of a series of three or more alternative genes resulting from mutations at the same locus on the chromosome. See page 65.

Multiple factors. Factors which act cumulatively in the determination of a character.

Mutation. A sudden change in the hereditary material. Frequently used in the restricted sense of a change in a single gene. Sometimes applied to the individual resulting from such change.

Normal distribution. See page 107.

Nucleus (plural *nuclei*). Specialized denser part of the protoplasm of the cell containing the chromosomes.

Ovule. The part of the ovary of a plant bearing an egg cell (ovum). It develops into a seed after fertilization of the egg cell.

Ovum (*or egg cell*). Female gamete.

Performance tests. See page 139.

Phenotype. The appearance of the individual as distinct from the genetic composition (genotype).

Pituitary gland. See page 81.

Protoplasm. The living substance of an organism.

Pure line. A stock essentially homozygous for all genes, normally produced by self-fertilization or close inbreeding.

Recessive character. One which is apparent only when the determining genes are in the homozygous state.

Regression. See page 111.

Segregation of factors in gametes. The separation of allelomorphs into different gametes (a fundamental principle of Mendelism).

Sex cell (*or gamete*). A reproductive cell.

Sex chromosomes. Those concerned with the determination of sex. See " x chromosome " and " y chromosome " and page 67.

Sex linked gene. One carried in the x chromosome.

Siblings. Children of the same parents.

Sperm (*or spermatozoon ;* plural, *spermatozoa*). Male gamete.

Sport. A new type of plant or animal due to mutation.

Unconditioned reflex. See page 176.

Uni-ovular twins. See " monozygotic twins."

X chromosome. The chromosome determining sex. See page 67.

Y chromosome. The chromosome which in one sex is a partner to the x chromosome.

Zygote. Fertilized cell (the union of two gametes).

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